RM-75-44

STABILITY IMPLICATIONS OF DISPERSAL LINKED ECOLOGICAL MODELS

Dixon D. Jones

August 1975

Stability Implications of Dispersal Linked Ecological Models

Dixon D. Jones*

Abstract

This paper examines an experiment designed to isolate and investigate the effects of space in ecological processes. As a corollary, and by necessity, the time dimension is considered. Traditional analytic models look primarily at this dimension. The scheme used seeks to add space in a manner that will not compound the time aspect of the process.

A hypothetical system was designed and observed for a finite selection of conditions. The Lotka-Volterra (L-V) predator-prey model is consciously selected as a starting point. Observations are examined in the light of available experience and ecological folklore and dogma. Conclusions are reached that apply not only directly to the two compartment dispersal situations depicted in this study, but also whenever mathematics is applied to ecology.

IIASA Overture

The accompanying paper is not applied systems analysis. The landscape is littered with systems that have been applied to after the wrong analysis. This is offered to the IIASA literature not as a bit of ecological esoteria but as a caveat to those who would neglect some critical dimensions of their problem because it is traditional to do so.

Spatial effects are implicit in the climatic studies of the energy project; they are inseparable from any real regional watershed problem; they are inextricably interwoven in the budworm study; national settlement systems are spatially dynamic; and economics should take seriously the lesson taught by Hotelling's optimizing (and ergo unstablizing) ice cream vendors.

---

*International Institute for Applied Systems Analysis, Laxenburg, Austria, and the Institute of Resource Ecology, University of British Columbia, Vancouver, Canada.

I. Introduction

Ecological systems are not concentrated at a single point. Not all have equal access to all points, contrary to the implications of most models of population dynamics. These models often imply that all interactions occur as if at one location, or at least as if distribution were random.

Attempts to simulate mathematical equations with laboratory organisms usually meet with failure. Coexistence or long-term persistence is difficult to achieve in a test chamber. Some reported successes in maintaining coexistence in a homogeneous environment have later been explained by the existence of refugia in the microstructure of the supporting media.

Gause (1934) could maintain a system of *Paramecium caudatum* (prey) and *Didinium nasutum* (predator) only by occasional reintroduction of prey.

The classic experimental work of Huffaker (1958) explicitly avoided spatial homogeneity. His work was notable for the elaborate efforts required to prolong the persistence of his predator-prey system. Huffaker relied on the manipulation of the physical complexity of his universe and on the relative dispersing abilities of his beasts.

Recently, Luckinbill (1973) reported on the maintenance of a homogeneous laboratory predator-prey system through the alteration of dispersal powers and the amplification of the nonlinear effects of prey food limitation. He still had space even though there was spatial uniformity. The dispersal process, which he influenced was possible because of the three-dimensional nature of the Petri dish.

Coexistence of laboratory predator-prey systems has relied on: a) refugia for the prey, b) "immigration" or reintroduction of prey from outside the system, or c) manipulations of the environment, as for example, by physical heterogeneity that gives a dispersal advantage to the prey. All support the opening postulate: ecological systems are not concentrated at a single point.

Perhaps the most common and intuitively acceptable impact of space on population stability is the process of "local extinction and re-immigration". One can verbally argue that if some statistical measure of re-immigration probability exceeds some measure of extinction probability, the whole system will survive even if isolated subregions do not. Analytic and experimental complexity make this a difficult concept to define. Insular population patterns are often interpreted in this view. (Mac Arthur and Wilson, 1967, and Simberloff and Wilson, 1970.)

Maynard Smith (1974) has simulated a 25-cell arena with predators and prey subject to stochastic dispersal. He concludes that permanent coexistence is favored by: a) highly mobile prey, b) some refuge for prey, c) restriction of the period of predator migration, and d) a large number of cells.

The above situations provide some believable notions on how space interacts with biological processes. But, for my own satisfaction, I would like to look for more generality. There remains a nagging question stemming from the discrepancies between theory and observation: does the mere existence of a spatially extended environment fundamentally influence the behavior of ecological systems?

There is no obvious *a priori* mechanism that is intuitive to me. Besides the lack of correspondence between point models and reality, there is little firm evidence to suggest the possible effects that space might have on ecological processes. A provocative situation is the planktonic patches in the open ocean. Steele (1974 a and b) has proposed an explanation for the formation of these patches despite a lack of observable gradients in the physical environment. His formulation links dynamic biological processes with environmental random turbulent diffusion. The results are different from "dimensionless" models.

It has been suggested that environmental heterogeneity--in either space or time--can lead to the maintenance of genetic heterozygosity in populations. (McDonald and Ayala,1974). Recently, Jones (1974) suggested that geographical separation, without environmental dissimilarity, can lead to the formation of differing gene frequencies in the populations of molluscs that he studied.

The purpose of this paper is to consider the creation of a situation where the effects of space could be isolated from the effects of biology. Supposedly, time and space are in some manner interchangeable, and conclusions from one can be applied to the other. May (1973) points to the errors caused by assuming that systems can be equally effective at "spreading the risk" in space and in time. Another clue to possible dissymmetry can be found in the problems that arise when the techniques of time series analysis are applied to spatial data (Granger, 1969). My own intuition says that spatial effects differ from temporal ones since an animal can visit a coordinate of space many times, but a coordinate of time only once. However, the cyclic effects of seasonality may soften this dichotomy. This issue will not be resolved here; however, the duality of space and time--or the lack thereof--underlies much of the following report.

II. The Scheme

The idea was to be as simple as possible: combine the simplest model with the simplest spatial arrangement and observe the results. It is simple but not analytically trivial. For this reason a program of experimental observation is adopted here. An analytic investigation should be the next step. A hypothetical system was designed and observed for a finite selection of conditions. (This may be an example of computerized natural history or perhaps of natural history on a computer.) Despite the lack of completeness that an analytic treatment would give and the lack of concreteness that more realism would provide, the observations presented will jostle several bits of ecological dogma and folklore, as well as present an interesting set of questions and considerations.

Consider two locations or "sites", identical and each with the same ecological operations occurring on it. A predator-prey system is used because of its dynamic nature and familiarity. Now join these two sites in a manner that allows an interchange of the predators and the prey. What does this do to the total system? Specifically, what does the interconnection do to the stability properties of the total system?

The physical arrangement is shown in Figure 1. The two sites are separated vertically. Site 1 contains the predator population x_1 and the associated prey population x_2. Site 2 contains predator x_3 and prey x_4. Between each two of these populations there is a "gate" that allows interaction (except diagonally). These gates can be opened and closed and the amount of interaction regulated.

Before specifying either the form of the predator-prey process or the style of the dispersal, we should examine some of the available experience and folklore to obtain insight and "predictions". It is commonplace to extrapolate beyond a particular situation and to propose general conclusions. To apply these conclusions to another real situation (in this case our current "experiement"), the conditions and assumptions need to be bent. In the following section, I ask you to suspend your objections to the contortions and to recognize the pseudo-dogma involved. My contention is: when I claim that Figure 1 "acts as if" it met the prerequisites of a particular notion, I am in no more error than when this is done with a real ecosituation.

III. Suggested Notions, Folklore and Dogma

The availability of refugia for prey leads to prolonged

persistence of laboratory microcosms. If we isolate predator x_3 by closing the gates to his compartment, location x_4 "acts as if" it were a refuge for prey x_2. The converse could be done by isolating predator x_1. (The dogma says that these acts should have a stabilizing effect on the system.) Now, if all gates are open, each of the prey locations acts as a refuge for the other. Because each of the refuges is subject to the predation of that site, the protection is not complete. But, if the predator populations x_1 and x_3 are properly imbalanced, there might be a net effect towards stabilization. The effect of the concurrent predator "refuges" is not clear.

The relative magnitudes of dispersal have been shown to affect persistence. We should, therefore, expect that if the prey disperse more easily than the predators, stability will be enhanced. We can expect the opposite if the predators are the movers. This is an easily testable situation. Accordingly, balanced dispersal should produce no global change.

The above perspectives are spatial. It is possible to cast the argument in a temporal framework. Consider the following: some x_2 move over and become x_4, and later some of these x_4 (domestic and foreign) move across and become x_2. In other words, there is a built-in time delay caused by the back and forth movement. Meanwhile, some of the x_4 were eaten by x_3; later the x_3 moved over to become x_1 which ate some of the remaining brothers in x_2. This has a negative effect on x_2, but the time constant is longer than the x_2-x_4 link. While there are no ingredients for a clear-cut time-lag situation, our experiment "acts as if" dispersal were creating a time-delay correlation for each of the populations.

According to dogma, if time constants in the delays are longer than the natural period of the system, the system is likely to be unstable. The natural time constant is on the order of the reciprocal of the birth and death rates; the time constant of delay is on the order of the reciprocal of the dispersal rate squared. If the disperal is slow compared to the birth rate, we have potential instability.

Before being labeled a "fuzzy thinker", I should say that I share whatever reservations you may have. The above three notions are indeed contradictory. My reason for presenting them is to provide alternate prospectives as background for our experiment. Time-lags, refugia, and relative dispersal rates are familiar elements of the theology of ecological stability. We should ask, when we are finished and know the outcome how Figure 1 resembles any of these factors.

One final consideration involves synchrony. If the sites are equivalent, if the dispersal is isotropic, and if the populations are in the same initial state, the two sites should remain equivalent for all time. The important question is whether or not dispersal tends to pull unmatched populations into synchrony. Maynard Smith (1973) concludes that synchrony will be promoted if prey (predators) move away from regions with abundant prey (predators). There is no phasing effect if prey (predators) move away from regions with abundant predators (few prey).

Maynard Smith's conclusions were drawn from graphical arguments for limit cycle oscillations. The wording of the conditions sounds as though dispersal requires a population to census itself. However, his conditions apply whenever they occur even if by accident. If dispersal were strictly random, we would see the net effect of time spent in each of the conditions. Later we shall relax the limit cycle requirement and observe the results.

IV. Methods and Materials

The real estate depicted in Figure 1 is general; the population dynamics and dispersal functions are as yet unspecified. There are infinite possible combinations. Where to begin? Because we want to explore the effects of linking the two sites, it is advisable to reduce all other complicating factors.

The simplest predator-prey model is the one credited to Lotka and Volterra (L-V). Namely:

$$\frac{dN_1}{dt} = + \alpha_1 N_1 - \beta_1 N_2 N_1 \quad ,$$

and (1)

$$\frac{dN_2}{dt} = - \alpha_2 N_2 + \beta_2 N_1 N_2 \quad ,$$

where N_1 is the prey population and N_2 the predator. The L-V model has received exhaustive treatment and comment in the literature. May (1973), for example, refers to its "pathological" neutral stability which breaks down with infinitesimal changes in its functional structure. Hirsch and Smale (1974, p.187) make a similar suggestion. The overriding lack of experimental and observational verification forces us to consider this model as a starting point at best.

Some of the shortcomings of the L-V model provide the incentive for its present use. First, it is simple and its properties are well known. The right-hand side of system (1) can be thought of as the first two terms of a Taylor expansion of the "true" function. (According to this view the inadequacies of system (1) imply that the higher order terms dictate the subtleties of behavior--a situation not common in most classic physical systems.)

Secondly, the neutrally stable property of system (1) places it at the balance between the qualitatively distinct states of inward and outward spiraling. If the spatial linkage changes the dynamics, this system should easily detect this change.

The system of equations used throughout is:

$$\begin{aligned}
\dot{x}_1 &= a_1x_1 + b_1x_1x_2 - D_1(x_1) + D_3(x_3) \quad , \\
\dot{x}_2 &= a_2x_2 + b_2x_2x_1 - D_2(x_2) + D_4(x_4) \quad , \\
\dot{x}_3 &= a_3x_3 + b_3x_3x_4 - D_3(x_3) + D_1(x_1) \quad , \\
\dot{x}_4 &= a_4x_4 + b_4x_4x_3 - D_4(x_4) + D_2(x_2) \quad .
\end{aligned} \tag{2}$$

The functions $D_i(x_i)$ are the amount of x_i that leaves "box i" per unit time. Various forms of $D_i(x_i)$ are possible; those used are described shortly.

The parameters (a_i,b_i) form an eight-dimensional space that would be tedious to explore. Because system (1) is know to be qualitatively insensitive to choice of $\alpha_i,\beta_i>0$, we shall assume that system (2) will also be. (However, the validity of this assumption will be probed.) We begin by setting:

$$a = \begin{pmatrix} -1 \\ +1 \\ -1 \\ +1 \end{pmatrix} \qquad b = \begin{pmatrix} +1 \\ -1 \\ +1 \\ -1 \end{pmatrix} \quad . \tag{3}$$

The eight functions $D_i(\cdot)$ form an eight-dimensional function-space that would be impossible to examine completely. For observational purposes, we severely limit the range of options

to be considered. The first restriction is that both sites have functionally equivalent dispersal. That is:

$$D_1(\cdot) = D_3(\cdot) \quad ,$$

and (4)

$$D_2(\cdot) = D_4(\cdot) \quad .$$

Often, but not always, we keep:

$$D_1(\cdot) = D_2(\cdot) = D_3(\cdot) = D_4(\cdot) \quad . \tag{5}$$

Additionally, the dispersal functions used will have only one free parameter, k_i, the dispersal coefficient. The value of k_i has the interpretation of dispersal strength. Further, the range of k_i is restricted to $0 \leq k_i \leq 1$. In the first round of "experiments" we have:

$$k_1 = k_3 \quad ,$$

and

$$k_2 = k_4 \quad .$$

The first test of system (2) requires a balanced grid with:

$$(a_1, b_1, k_1) = (a_3, b_3, k_3) \quad ,$$

and (6)

$$(a_2, b_2, k_2) = (a_4, b_4, k_4) \quad .$$

IV.1 Types of Dispersal

I have selected seven functional types of dispersal for this experiment. (The "type" refers to functional forms of exchange between sites.) My apologies to the reader for nomenclature--it was derived as implemented as opposed to logical presentation. The seven types are defined as follows:

Type I: Proportional

The rate of dispersal $D_i(x_i)$ is taken as a constant fraction

of the population. That is:

$$D_i(x_i) = k_i x_i \quad . \tag{7}$$

Because k_i is a rate, $k_i<1$ is not required. That restriction is only equivalent to the dispersal rate being less than the intrinsic population rates a_i and b_i. This restriction will be tested by relaxation.

Type II: Proportion of Excess

The normal equilibrium levels for system (2), with (3), is $x_i = 1$. Dispersal is restricted to the excess above equilibrium. That is:

$$D_i(x_i) = k_i(x_i - 1) \quad , \text{ if } \quad x_i \geq 1 \quad ,$$

and (8)

$$D_i(x_i) = 0 \quad , \qquad \text{if} \quad x_i<1 \quad .$$

Type III: Global Escape/Pursuit

Type III implies that the dispersers can perceive the magnitude of the other species in both sites. Movement is then proportional to the fraction of the other species in the site of interest. That is, the predator in Site 1 will move to Site 2 in proportion to the share of prey currently in Site 2 (or visa versa). Or:

$$D_1(x_1) = k_1 \frac{x_4}{x_2 + x_4} \cdot x_1 \quad ,$$

and (9)

$$D_3(x_3) = k_3 \frac{x_2}{x_2 + x_4} \cdot x_3 \quad .$$

Similarly, prey move away from excess predators as:

$$D_2(x_2) = k_2 \frac{x_1}{x_1 + x_3} \cdot x_2 \quad ,$$

and (10)

$$D_4(x_4) = k_4 \frac{x_3}{x_1 + x_3} \cdot x_4 \quad .$$

Type IV: Local Escape/Pursuit

Type IV assumes that dispersal rates are a function of the level of the other species only in their own site. In order to scale dispersal rates between 0 and 1, an exponential form is used. For predators:

$$D_i(x_i) = x_i (1 - (1 - k_i)^{x_{i+1}}) \quad , \qquad (i = 1,3) \qquad (11a)$$

and, for prey,

$$D_i(x_i) = x_i k_i^{x_{i-1}} \quad , \qquad (i = 2,4) \quad . \qquad (11b)$$

When the assessed population is at its equilibrium; that is:

$$x_{i\pm1} = 1 \quad ,$$

the dispersal rate for population i is k_i.

Type V: Nonlinear Density Dependence

The dispersal rate for Type V depends only on x_i; it is a monotonically increasing function of local population. The form used is:

$$D_i(x_i) = x_i (1 - (1 - k_i)^{x_i}) \quad . \qquad (12)$$

Again,

$$D_i(1) = k_i \quad .$$

For all of the above five dispersal types, the condition:

$$0 \leq \frac{D_i(x_i)}{x_i} \leq 1 \qquad (13)$$

on the "rate per capita" holds as long as $0 \leq k_i \leq 1$. Types III and IV are nonlinear and will require another parameter if we relax condition (13). Types VI and VII, mentioned below, are not restricted by (13).

Type VI: Linear Escape/Pursuit

The dispersal rate for Type VI increases linearly with the level of the other species in the site of interest. That is:

$$D_i(x_i) = k_i x_j x_i \quad , \tag{14}$$

where the cyclic condition

$$j = i - 1 \ , \quad \text{if } i > 1 \ ,$$

and

$$j = 4 \ , \quad \text{if } i = 1$$

holds.

Type VII: Linear Density

The dispersal rate for Type VII increases linearly with density. Or:

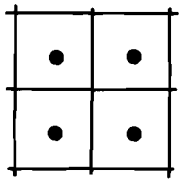
$$D_i(x_i) = k_i x_i^2 \quad . \tag{15}$$

All seven dispersal types are summarized in Table I.

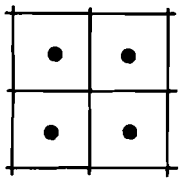
A Fortran program was written for the IIASA PDP-11 to numerically integrate system (2) for all seven dispersal types described in the previous section. The algorithm used was the Adams-Bashforth predictor-corrector with a second order Runge-Kutta algorithm providing the start-up values. A time step of 0.05 was used. The results and figures reported in the following sections utilized this program.

Table I.

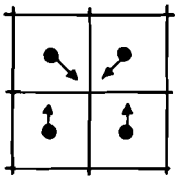
DISPERSAL TYPES

I 

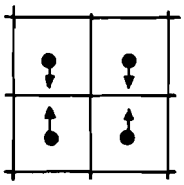
$$D_i(X_i) = X_i \cdot k_i$$

II 

$$D_i(X_i) = (X_i - 1) \cdot k_i \qquad (D_i(X_i) \geq 0)$$

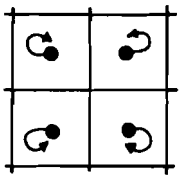
III 

$$D_i(X_i) = X_i \cdot k_i \cdot \frac{X_{i-1}}{X_{i-1} + X_{i+1}}$$

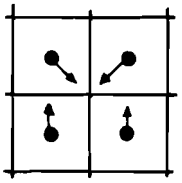
IV 

$$D_i(X_i) = X_i \cdot (1 - (1 - k_i)^{X_{i+1}}) \qquad i = 1,3$$

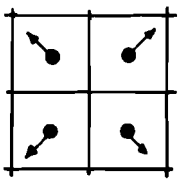
$$D_i(X_i) = X_i \cdot k_i^{X_{i-1}} \qquad i = 2,4$$

V 

$$D_i(X_i) = X_i \cdot (1 - (1 - k_i)^{X_i})$$

VI 

$$D_i(X_i) = X_i \cdot k_i \cdot X_{i-1}$$

VII 

$$D_i(X_i) = X_i \cdot k_i \cdot X_i$$

V. Results: Phase 1

In Phase 1, the grid is balanced according to (6), with a_i and b_i set as in (3). The k_i's form a two-dimensional parameter space. Five primary dispersal sets are used to bound the exploration of this space. They are given in Table II below.

Table II

k_i set	1	2	3	4	5
Pred (k_1,k_3)	0.5	0.9	0.0	0.9	0.1
Prey (k_2,k_4)	0.5	0.0	0.9	0.1	0.9

Sets other than the above five have been used to refine and to test conclusions as needed. The initial conditions $x_i(t=0)$ form another four-dimensional space.

It is an extremely inefficient proposition to grope among all possible combinations of a_i, b_i, k_i, x_i (0) as well as $D_i(\cdot)$. A more analytic procedure could quickly, (hopefully), and more compactly provide conclusions. This "natural history" route is attempted only as a first step to gain insight and to guide further analytic work.

We limit our search of possible initial conditions by starting each time with an equal number of "animals". Shifts in apportionment between the two sites are explored.

At global equilibrium there are:

$$x_1^* + x_3^* = 2 \text{ predators,}$$

and

$$x_2^* + x_4^* = 2 \text{ prey.}$$

In the following cases, the starting level is taken as twice the equilibrium level. That is, all initial conditions satisfy:

$$x_1(0) + x_3(0) = 4 \quad ,$$

and (16)

$$x_2(0) + x_4(0) = 4 \quad .$$

There is an infinity of combinations that satisfy condition (16). However, the "initial condition-space" has been reduced to two dimensions. We select five primary sets of conditions to span the extreme possibilities. The "condition diagram" illustrated in Figure 2a shows the k_i and $x_i(0)$ values in any given case. Figure 2b repeats the sets of k_i values given in Table II; Figure 2c shows the primary sets of initial conditions, $x_i(0)$.

The output of interest is the average (or total) population for the whole system. Graphic solution phase-plots used the variables:

$$P(t) = \tfrac{1}{2}[x_2(t) + x_4(t)]$$
$$= \text{average prey per site}$$

and (17)

$$Q(t) = \tfrac{1}{2}[x_1(t) + x_3(t)]$$
$$= \text{average predators per site.}$$

For each case, $x_i(t)$ values were printed at increments of $\Delta t = 0.5$. The referent system time scale is the period of a full cycle. For parameter values (3) this is $\tau \simeq 7$. The magnitude of dispersal was recorded as:

$$D13 = D_1(x_1) - D_3(x_3) \quad ,$$

and (18)

$$D24 = D_2(x_2) - D_4(x_4) \quad .$$

Of special interest is the maintenance or "stability" of the L-V characteristics. An important property of the cycles of L-V system (1) is the constancy of the quantity:

$$G = \beta_2 N_1 - \alpha_2 \log N_1 + \beta_1 N_2 - \alpha_1 \log N_2 \quad . \tag{19}$$

(Kerner (1972), Maynard Smith (1974), Hirsch & Smale (1974)). There are four significant functions of the form (19): one for Site 1, one for Site 2, one for the combined system, and one for the system of P, Q. Symbolically, these are:

$$G12 = -b_2 \cdot x_1 - a_2 \cdot \ln x_1 + b_i \cdot x_2 + a_1 \cdot \ln x_2 \quad , \tag{20}$$

$$G34 = -b_4 \cdot x_3 - a_4 \cdot \ln x_3 + b_3 \cdot x_4 + a_3 \cdot \ln x_4 \quad , \tag{21}$$

$$G = G12 + G34 \quad , \tag{22}$$

$$GPQ = \bar{\beta}_1 \cdot P - \bar{\alpha}_1 \cdot \log P + \bar{\beta}_2 \cdot Q - \bar{\alpha}_2 \cdot \log Q \quad , \tag{23}$$

where

$$\bar{\alpha}_1 = -(a_1 + a_3)/2 \quad , \qquad \bar{\beta}_1 = (b_1 + b_3)/2 \quad ,$$

$$\bar{\alpha}_2 = (a_2 + a_4)/2 \quad , \qquad \bar{\beta}_2 = -(b_2 + b_4)/2 \quad .$$

The phase trajectories of the P,Q system are the major references for judging system behavior. These are often supplemented by the actual $x_i(t)$, D13, D24 and "G" values to make a final diagnosis.

System (2) with no dispersal serves as our references. The phase plot is shown in Figure 3. Sites 1 and 2 operate as mirror images with no interaction. The G values are:

$$\begin{aligned} GPQ &= G12 = G34 = 2.6137 \\ G &= G12 + G34 = 5.2274 \quad . \end{aligned} \tag{24}$$

Since all initial conditions will be set at (P,Q) = (2,2), both Figure 3 and (24) will be important for comparisons.

Over 200 cases have been tried in order to investigate the dispersal types described so far, and to obtain the elaborations described below. Work began with a thorough look at combinations of k_i and $x_i(0)$ sets for Type I. Many case options were found to be redundant with respect to the stability properties of the system. Therefore, the variety of options narrowed as time progressed. The possibility exists that critical cases were overlooked--especially for the more complex cases described in later sections. For example, some type of resonance behavior is hypothetically possible. Since none has so far been observed, the possibility is less likely although has not yet been eliminated

Results from this work indicate that the L-V system is not fragile with respect to the structural changes of system (2). In nearly all cases, the system evolved into a synchronous pair of L-V systems with zero net migration. In many cases the transient decayed rapidly (on the order of one cycle); an illustration is given in Figure 4. (Figure 4 is a composite of dispersal Types I through VII, all using the case [1,a] referred to in Figure 2.) There is a modest variation in the position of the equilibrium cycle. In each case GPQ is shown as an indication of cycle displacement.

A number of cases were run for each of the seven dispersal types. Several cases did not evolve to an L-V system, but instead became unstable or spiraled down toward $x_i = 1,(i=1,...,4)$; two typical examples are shown in Figure 5. Note the dispersal strengths in these two cases. The obvious conclusion is that prey mobility is destabilizing, while predator mobility is stabilizing--a clear contradiction to Huffaker's experiment. However, there is another explanation.

The cases identified as unstable were all [3,a] or variations of it. Each of the dispersal types was unstable for this case. With the exception of Type III all other types were stable for Case [2,a] and its variants. An examination of both of these behavior states shows them to be critically sensitive to changes in initial conditions. In each of the unstable cases, a combination of initial condition and dispersal parameters excludes predators from one of the sites. Thus, prey entering this site are unmolested and grow exponentially.

In Case [2,a], for example, no prey can get into Site 1; therefore this site becomes a sink for predators. The continual uncompensated loss of predators in Site 1 damps the system down to the equilibrium. This behavior is critically sensitive to changes in initial conditions. If all compartments begin with non-zero populations, the system will evolve in the style shown in Figure 4.

Stable or unstable cases are imitations of a refuge configuration. By changing a few parameters in the integration program, we can look more thoroughly at the refuge effect. Those observations will be given in the next section; first we should look at the transient behavior of those cases that go to L-V cycles.

One of the quantities computed is GPQ, given in equation (23). Any L-V cycle is characterized by GPQ = constant. Figure 6 shows a contour surface of constant GPQ. The minimum value is 2.0 at [P,Q] = [1,1].

An examination of all of the cases provides few clear trends. In Figure 4, the values range above and below the referent level

of GPQ = 2.61. In general, the more unbalanced the initial conditions (for example in Cases a, or c versus d or e), the larger the final deviation from 2.61. For all dispersal types every Case-3 and most Case-5 situations lead to a smaller final GPQ. The converse is true for Case 4 but not for Case 2. The two most extreme cases found are shown in Figure 7. Sofar as the system tends to shift the final cycle in or out, we can conclude that a relative superiority of prey dispersal is stabilizing, and superior predator dispersal is destabilizing.

V.1 Refuge Conditions

With only a slight alteration in system (2), we can create a single site with attached refuges. As regards Figure 1, we locate our L-V animals in Site 1 and let Site 2 be the potential refuge. To do this we close the gate between predator and prey in Site 2. That is, we set:

$$b_3 = b_4 = 0$$

in system (2).

To maintain visual consistency with the other examples, we use: $P(t) = x_2(t)$, and $Q(t) = x_1(t)$ in the phase plots. Initial conditions are set at $P(0) = 2$, $Q(0) = 2$. Initial conditions for x_3 and x_4 lead to four primary sets denoted r_i. These are:

r_1	r_2	r_3	r_4
2 0	2 2	2 0	2 2
2 0	2 0	2 2	2 2

The refuge conditions are specified as Type IR, Type IIR, etc. For Type IR, outcome is insensitive to initial conditions. The system is unstable for k-set 1,3,4 and 5, and stable for k-set 2, as shown in Figure 8.

The explanation for this behavior is similar to that given earlier: if only the predators have a refuge, this refuge acts as a dissipative sink for the system. However, the existence of a prey refuge is a population source that continually feeds the whole system.

Because the outcome for Type IR did not depend on initial conditions, only r_2 and r_4 cases were used for the remaining

trials. Type IIR dispersal did not differ from Type IR except that the stable case of k-set 2 was more strongly damped. Type IIIR was similar to Types IR and IIR with two exceptions: a neutrally stable orbit resulted from k-set 2, and a stable spiral resulted from k-set 3. In Type IIIR x_4 diverged except for Case $[2,r_2]$ when x_4 was kept identically zero. Type IVR were similar to Type IIIR, but the exceptional Cases 2 and 3 were reversed in behavior.

Type VR is qualitatively similar to Types IR and IIR, while Types VIR and VIIR are very different. Type VIR is stable in P,Q for k-set 3 (but with diverging x_4). Type VIR with, k-sets 1,2,4 and 5 lead to neutrally stable orbits, with x_4 highly oscillatory but not divergent. These orbits are eccentric with a predator average much greater than 1.0 (Figure 8c). The quadratic form of Type VIIR dispersal forces stability regardless of the values of the k_i parameters (Figure 8d).

Table III summarizes the results of the refuge (Class R) system. (A definition of "class" is given in the following section.) The stability of this system can be attributed to the "birth and death" processes that occur in the refuge. The next step was to suspend these processes within the refuge by setting:

$$a_3 = a_4 = 0$$

This class is denoted by "S" (e.g. Type IS). In all cases the entire system is constantly stable. A typical trajectory is shown in Figure 8e.

VI. Extensions and Expansions

Sofar we have arranged our arena of observation so that it is staticly balanced. The population dynamics on each side are identical (relaxed, however, to mimic refugia). We have also maintained a functional and parametric balance between sites. In this section we shall look at a few elementary non-symmetric cases.

The classification of "types" of dispersal can be considered a vertical stratification in our "exploration-space". The examples used are given in Table I. We now introduce a horizontal axis of class of dispersal.

Class R

TYPE	Primary k - set 1	2	3	4	5
I	U	S	U	U	U
II	U	S	U	U	U
III	U	U	S	U	U
IV	U	S	N*	U	U
V	U	S	U	U	U
VI	N	N	S*	N	N
VII	S	S	S	S	S

Class S

TYPE	Primary k - set 1	2	3	4	5
I					
II					
III					
IV					
V					
VI					
VII					

STABLE

Table III. The stability results for refuge Classes R and S.

N = neutrally stable orbit; S = spiral toward an equilibrium; U = unstable spiral. The "*" indicates that the refuge prey population diverged. The primary k-sets are given in Figure 2b.

VI.1 Classes of Dispersal

A class does not specify a functional form but defines some feature of dis-symmetry. Classes are denoted by capital letters, as for example, "Type IR" and "Types IVS". Any type can be mixed with any class. The "null" class has been described in the previous section. Below are brief descriptions of four additional classes. The following section presents some results, primarily through examples.

Class A

We have assumed that the sites are equal: the population dynamics for each site is the same. In terms of L-V system (1), this means that the α's and β's are identical in Site 1 and 2. In reality, we do not expect to have perfectly matched parameter values. In Class A we shall allow one site to be "better" (or "worse") than the other.

At first glance it would seem that L-V system (1) has four independent parameters. But simple rescaling of N_1, N_2 and time can set three of the parameters to 1. This leaves one free parameter. In the full system (2), we do not scale each site independently, thus we still have five free parameters.

For simplicity (and out of faith), we alter only one parameter in one site. Since choice is arbitrary, we select the prey growth rate in Site 1 (a_2). Class A is defined by:

$$a_2 = 0.8 \quad .$$

Class B

Experience with system (1) suggests that system (2) has symmetric behavior with respect to a single parameter change. As insurance against surprise, Class B uses:

$$a_2 = 1.2 \quad .$$

A few random trials support the redundancy assumption of Class B.

Class C

Instead of unbalancing the population processes, we unbalance the dispersal. That is, the tendency to move (as measured

by k_i) is not identical in both directions. The most obvious natural analogy is the existence of a physical gradient across sites such as in a flowing stream. However, many subtle phenomena can influence the propensity to migrate, and we would expect these influences to vary spatially and isotropically.

Four k-sets are selected to span an interesting range of possibilities. These are:

k-set:	set 9:	set 10:	set 11:	set 12:
k_1 k_3	0.0 0.5	0.0 0.5	0.1 0.9	0.1 0.9
k_2 k_4	0.0 0.5	0.5 0.0	0.1 0.9	0.9 0.1 .

The above sets are included in Figure 2e.

Class D

Class D adds a switch that shuts off dispersal for animals which would find themselves in a "worse" location. That is, prey only move towards the site with the fewest predators, and predators only move towards the site with the most prey. Movement is according to the given type.

VII. Results: Phase 2

Classes A through D have been investigated for a number of cases in each of the types. The majority of interpretations are based on the case with balanced initial conditions (set b) with the exception of Class D). Other initial conditions were sporadically tried.

The conclusion derived from Classes A and B is simple:

Inequity leads to stability.

In all of the cases (except in the troublesome Case [3,a] discussed above), the unequal sites lead to a stable spiral towards (1,1). Figure 9 illustrates this action.

Class C relaxes the directional balance of dispersal. In some examples prey and predator move preferentially in one direction (k-sets 9 and 11). In other examples, the flow is

counter (k-set 10 and 12). Types I,II,IV,V and VII are in general stable. Neutrally stable orbits are generated under special conditions. Type VI always leads to a neutrally stable orbit. Further investigation found Type VI orbits not to be limit cycles.

Of all the combinations tried, only Type IIIC exhibits genuine instability over a range of parameter values. If the major flow is in the same direction for both predators and prey, some combinations of k_i produce increasing spirals (Figure 10a). Table IV shows the results of many combinations of k-values for Site 1 and 2. Only half of the array is shown because it is symmetrical about the diagonal. Results not tried, but safely assumed, are in parentheses.

Class D consistently shows neutral stability. An examination of G-values showed the orbits not to be L-V cycles. The flow back and forth did not die out as was found in our previous examples. A sample phase trajectory is shown in Figure 10b.

VIII. Conclusions

A number of general conclusions can be drawn from this investigation that not only apply directly to the two compartment disperal situation shown in Figure 1, but are also applicable whenever mathematics is applied to ecology. It might be argued that "conclusion" is too strong. Nevertheless, we can present some cautions related to the problems of matching theory with observation.

The direct observations have been discussed previously for each of the dispersal types and classes. They can be summarized as follows: when two L-V systems are coupled isotropically, the complete system evolves into a larger L-V system. Only in those situations where initial conditions prevent one of the dispersal directions from operating can there be stability or instability. As initial conditions become more unbalanced, the resulting cycle tends to deviate further from the balanced cycle (Figure 3). If prey dispersal exceeds predator dispersal, the final cycle tends to be smaller. This point is similar to Huffaker's conclusion: stability is promoted when the prey have superior dispersal powers.

However, even with isotropic dispersal, when two non-equivalent sub-systems are coupled, stability is the general rule. Only in those rare situations where initial conditions effectively isolate one of the prey populations (allowing it to grow exponentially), is instability a problem. It is almost an axiom of ecology that the parameters of two separate

k, Site 2

k, Site 1	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0		2.0	5.0	10.0
0.0	N	(u)	(u)	(u)	(u)	U	(u)	(u)	(u)	(u)	U		U	S	S
0.1		(r)	(u)	(u)	(u)	U	U	U	U	U	U		S	S	S
0.2			(n)	(u)	(u)	(u)	(u)	U	U	U	~N	...	S	(s)	(s)
0.3				(n)	(u)	U	U	~U	S	S	S		(s)	(s)	(s)
0.4					(n)	N	N	~S	S	S	(s)		(s)	(s)	(s)
0.5						N	N	S	S	S	(s)		(s)	(s)	(s)
0.6							(n)	~S	(s)	(s)	(s)		(s)	(s)	(s)
0.7								(n)	(s)	(s)	(s)		(s)	(s)	(s)
0.8									N	~S	S	...	(s)	(s)	S
0.9										(n)	~S		(s)	(s)	S
1.0											(n)		(s)	(s)	(s)

Table IV. The stability regions for Type IIIC dispersal. N = neutrally stable orbit; S = spiral toward an equilibrium; U = unstable spiral. The "~" indicates a process which is very slow in revealing itself. The (•) are results which were not tried but can be safely assumed. The array is symmetric about the diagonal.

systems will not be identical. Thus, even if animal populations obeyed exactly the rules of system (1), the discrepancy from place to place of the basic parameters would eradicate the "pathological" neutral stability inherent in the L-V system.

When we converted our system to a refuge situation, we found an exponential increase of prey in the refuge. Biological reality dictates that prey population growth is resource limited. One form of this limitation was used in dispersal Class S. Here we eliminated the birth and death processes in the refuge and obtained stability. None of the refuge cases maintained its neutrally stable behavior. Insofar as this situation is analogous to time delays, it is not capable of displaying the associated instabilities.

An interesting aspect of dispersal was observed in the examination of the refuge case; it was also apparent to a lesser extent in the other classes of dispersal. Dispersal Types I thru VI were linear (or less) with respect to the dispersing population. This was adequate in most cases to allow the net dispersal to decay to zero. For instance, dispersal Type I is equivalent to Fick's Law of diffusion processes. (This law is renowed for it ability to even out spatial distributions.) An implicit biological assumption of this linear (or less) dispersal is that crowding effects are absent.

Only Type VII dispersal was quadratic with respect to the dispersing population. The effect of this was to preferentially disperse away from "crowded" sites. The stabilizing effect of this was remarkable.

Now we shall illustrate some of the difficulties encountered and the observations made that although reflecting indirectly upon dispersal, bear more significantly on the fundamentals of mathematical ecology. Since this project was not designed to investigate these areas, the observations are only suggestive and indicate certain regions in which difficulties may arise.

It is customary in mathematical models for the variables to be densities, that is, numbers of individuals per unit area. Suppose the unit area of interest is the "site". The whole system in Figure 1 is two units of area. If, in Figure 1, there were no fences or barriers, we would have one system--system (1). The cycle in this case is the same as that shown in Figure 3.

Imagine a field situation where the observation area includes Site 1 and 2 shown in Figure 1. Suppose further that an ecologist has hypothesized that some model--e.g. the L-V system--is appropriate for his field animals, and he wishes to test his observations against that model. In this exercise, the computer animals actually perform in the same manner as

the model, and the correspondence is easy to verify. If data from the field situation are arranged on a phase plane (Figure 3), they coincide with the predictions of the L-V model. Obviously, here the correspondence is perfect.

The above example works because the area selected by the investigator coincides exactly with the area used by the "animals". That is, the density measure is the same for both observer and participants. The following example will illustrate what may happen if these two areas are not identical.

Again we have an investigator who treats Sites 1 and 2 as a single ecological unit. This time, however, the animals are restricted to only half of the area, unknown to the observer. (This can be done by putting all animals into one site and shutting the gates to the other.) Figure 10a shows the result of this process. Although the "true" system has been behaving as system (1), the effect of using an "improper" measure of area is to distort the cycle as shown in Figure 11a. The model prediction is Figure 11b.

There is a large discrepancy between Figures 11a and 11b. It could be argued that a more observant investigator would realize that his animals were using only half the field. It is not necessary to divide the populations strictly on a geographic basis. It need only be required that the individuals act as if they were restricted to a part of the entire region.

By a scaling of variables, it would be possible to obtain the proper density measurement in this example. The point is that such rescalings might always be necessary before the field data can be compared to a particular mathematical model. Furthermore, the proper choice of scale may not be knowable, and may, in fact, rely on some best-fit procedure.

It is not the intention of this paper to defend the L-V model. There are many reasons why the model is unrealistic. One of its critical features is its neutral stability as shown in Figure 3 (and equivalently in Figure 6). Because field data do not behave accordingly, the model is rejected. The model could also be (and is) rejected because its component parts fail to meet reality. Even in more "realistic" models, the test is often limited to a gross comparison with reality.

Let us again suppose that reality is in fact system (1). The field situation is as follows: there are two neighboring sites indistinguishable to the investigator. Further, for simplicity, there is no interchange between these sites. If both sites were equivalent, we would have Figure 3 (or Figure 11b). Matching observations to our model would be trivial. Suppose, however, that both subregions are not exactly equivalent, that is, one or more of the parameters differ between

the two subregions. If we plot our observations on the phase-plane, we obtain the peculiar trajectory of Figure 12. Based on the data obtained, we could easily guess at the conclusion--namely, that the system is highly stochastic. No further attempt would be made to develop a deterministic model.

What has happened in Figure 12 is that each of the sites is operating on a slightly different time period and thus its cycle is continually moving in and out of phase with respect to the other. We don't have to hypothesize two separate and distinct regions for this situation to occur. All that is necessary is that there be more than one sub-population operating on slightly different characteristics. This type of situation is surely the rule rather than the exception in ecology. Often, an overriding periodicity of the environment will tend to synchronize both sub-systems, although, the synchrony may not always be perfect.

The last example illustrates the perversity with which deterministic models can behave. Figure 12 could be unscrambled if all four state variables had been recorded rather than the species averages. Again, state variable identification and measurement are extremely important aspects of systems analysis and understanding.

We conclude with illustrations of the general perversity of this "simple" system in some of its wilder forms. Figure 12 is probably the strangest as well as the simplest in construction. Figure 13 is a composite of several of the unusual cases that arose during this investigation. They are offered primarily as entertainment and also as a warning of the problems of matching measurement with a hypothetical model.

On could pursue many additional types of dispersal. Before attempting this, however, one should step back and evaluate what has been done, and then approach the subject with a more specific question. An obvious situation that has not been attempted is the coupling of a stable system with an unstable one. This should be tried with a model that has more biological realism in its component parts. Finally, we have gone too long without taking an analytic look at the stability implications of ecological dispersal.

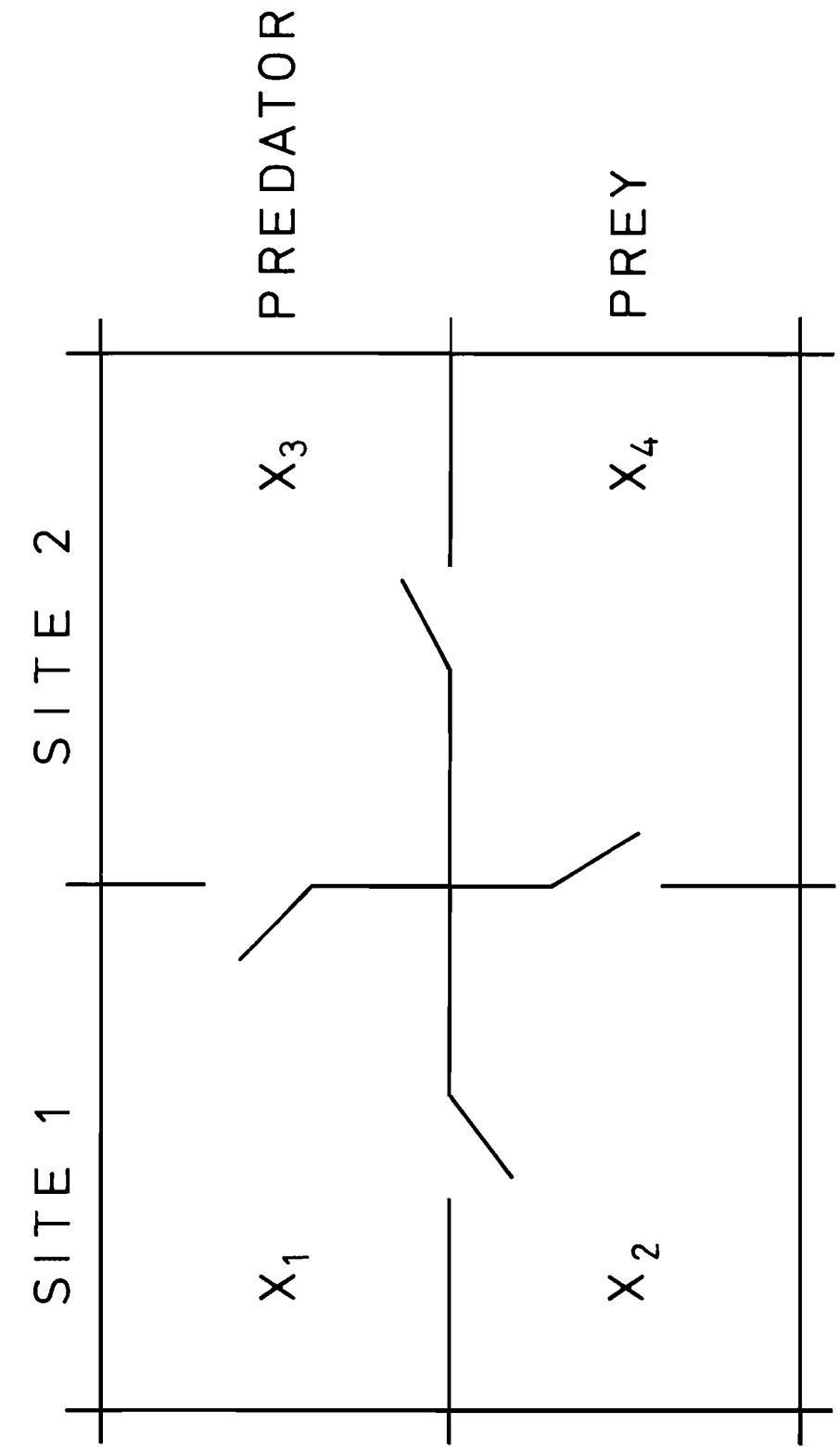
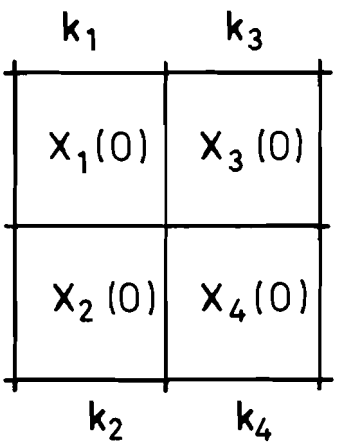


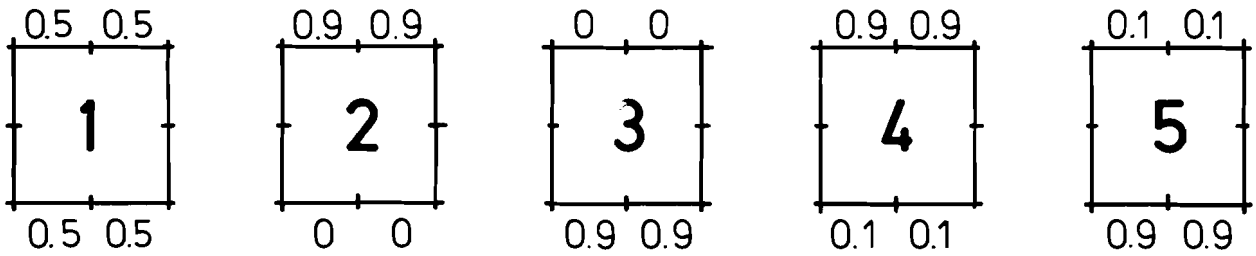
Figure 1. Two compartment dispersal "experiment".

a)



FORMAT FOR
DISPERSAL PARAMETERS
AND
INITIAL CONDITIONS

b) PRIMARY SETS OF DISPERSAL PARAMETERS



c) PRIMARY SETS OF INITIAL CONDITIONS

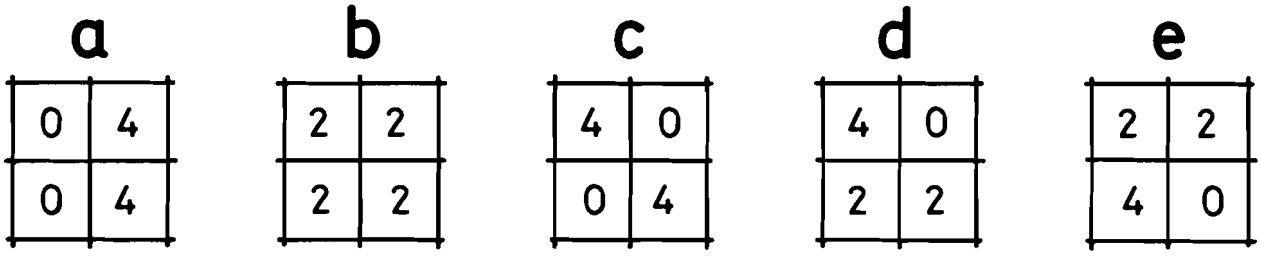
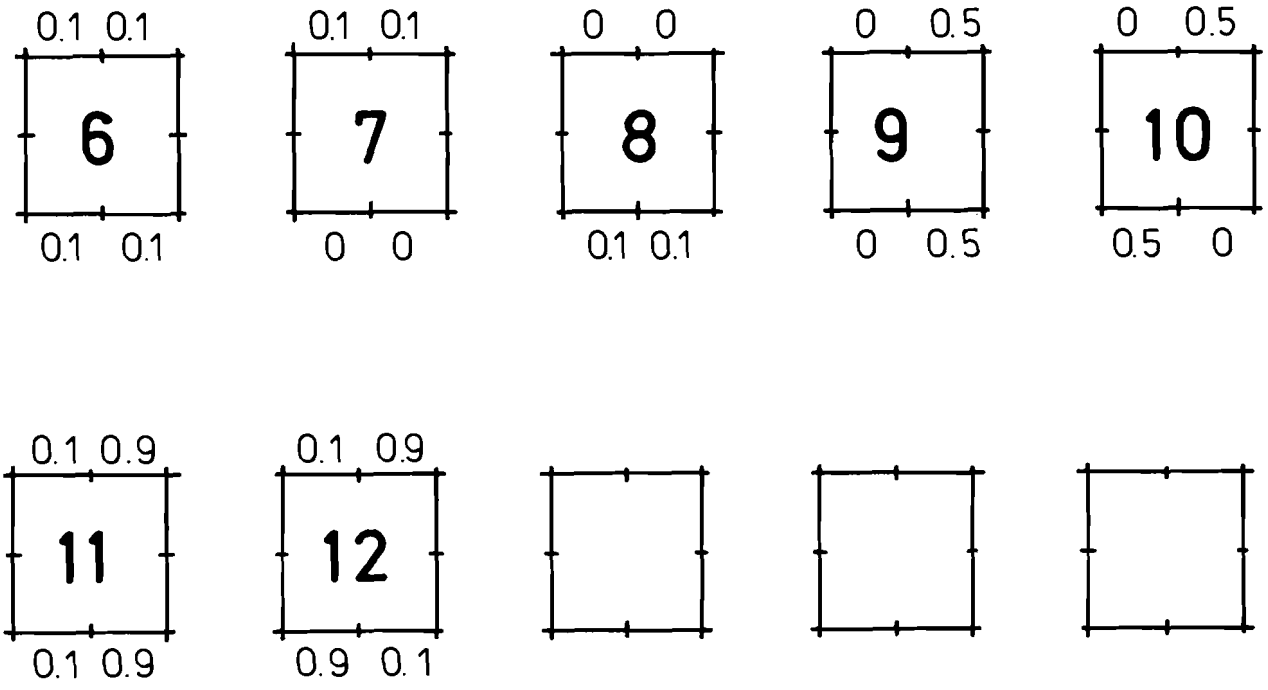


Figure 2.

d) ADDITIONAL k- SETS



e) ADDITIONAL X(0) - SETS

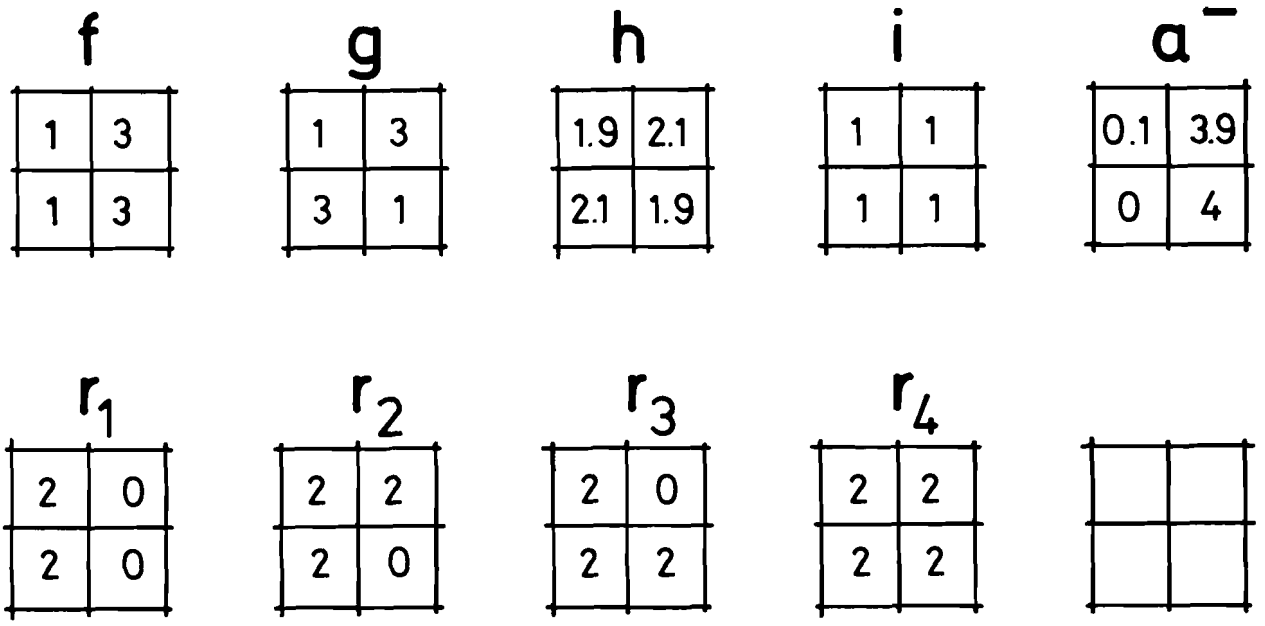


Figure 2. (continued)

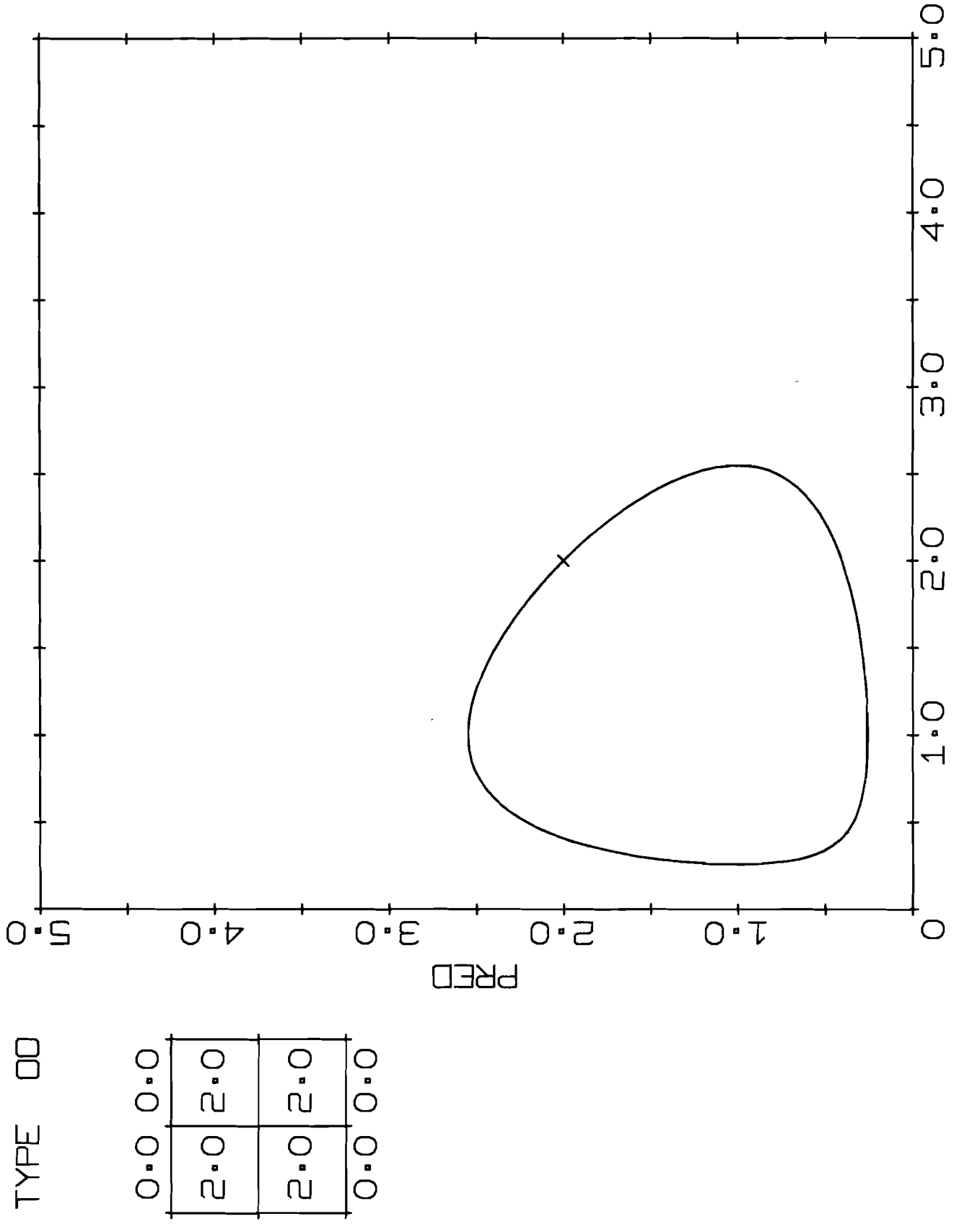


Figure 3. Reference phase trajectory with no dispersal. Predator and prey magnitudes are averages for both sites.

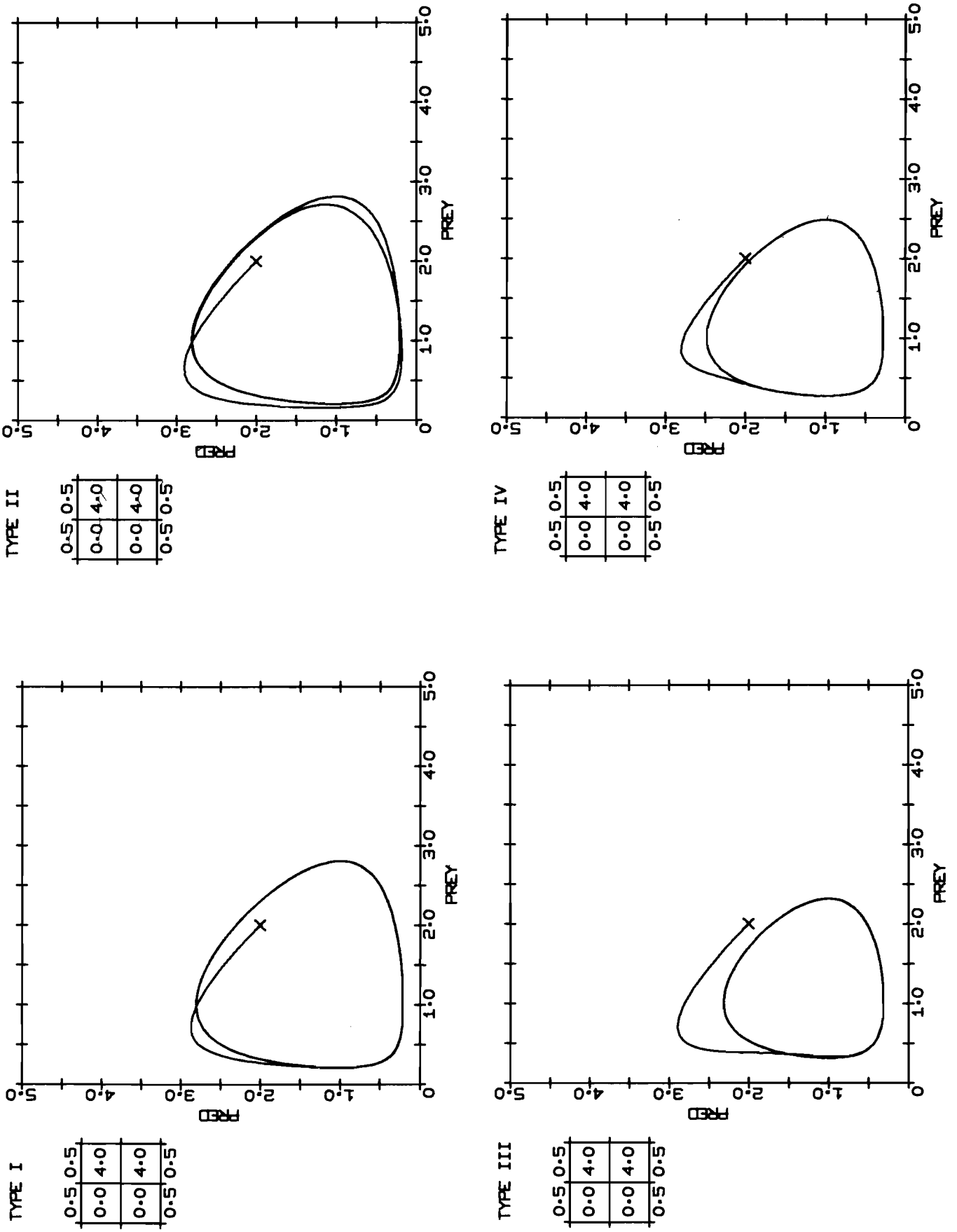


Figure 4. Typical behavior for each dispersal type when dispersal is balanced.

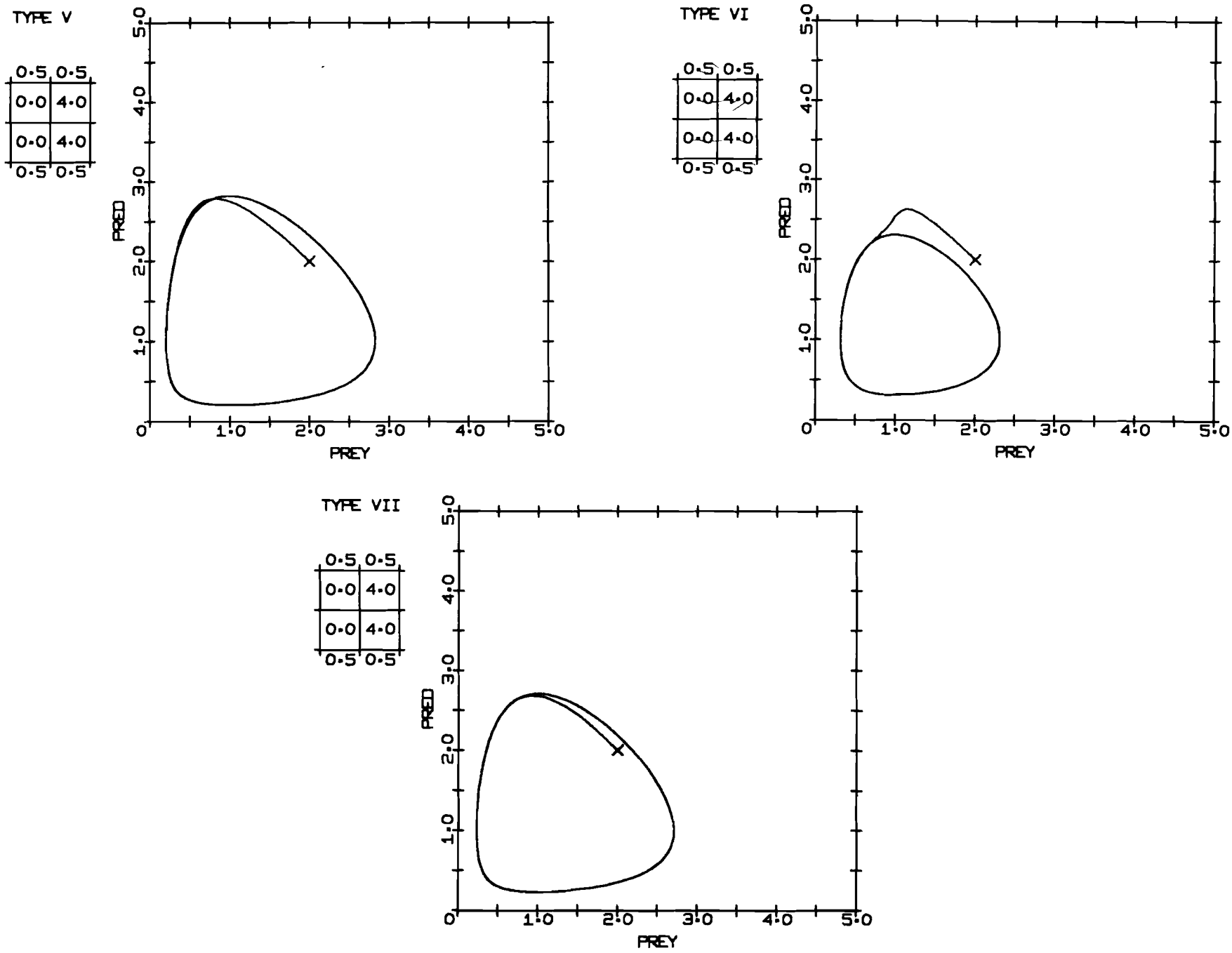
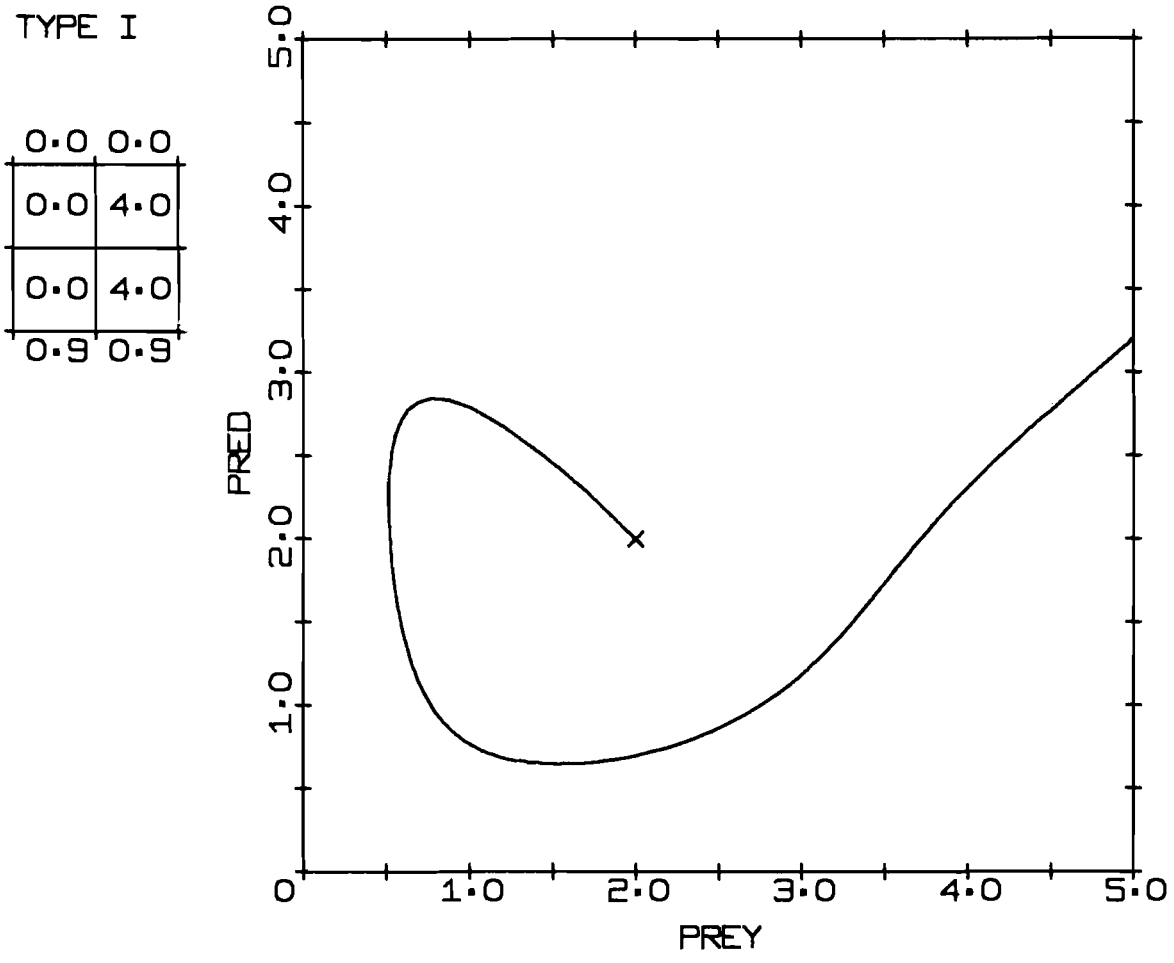


Figure 4. (continued)



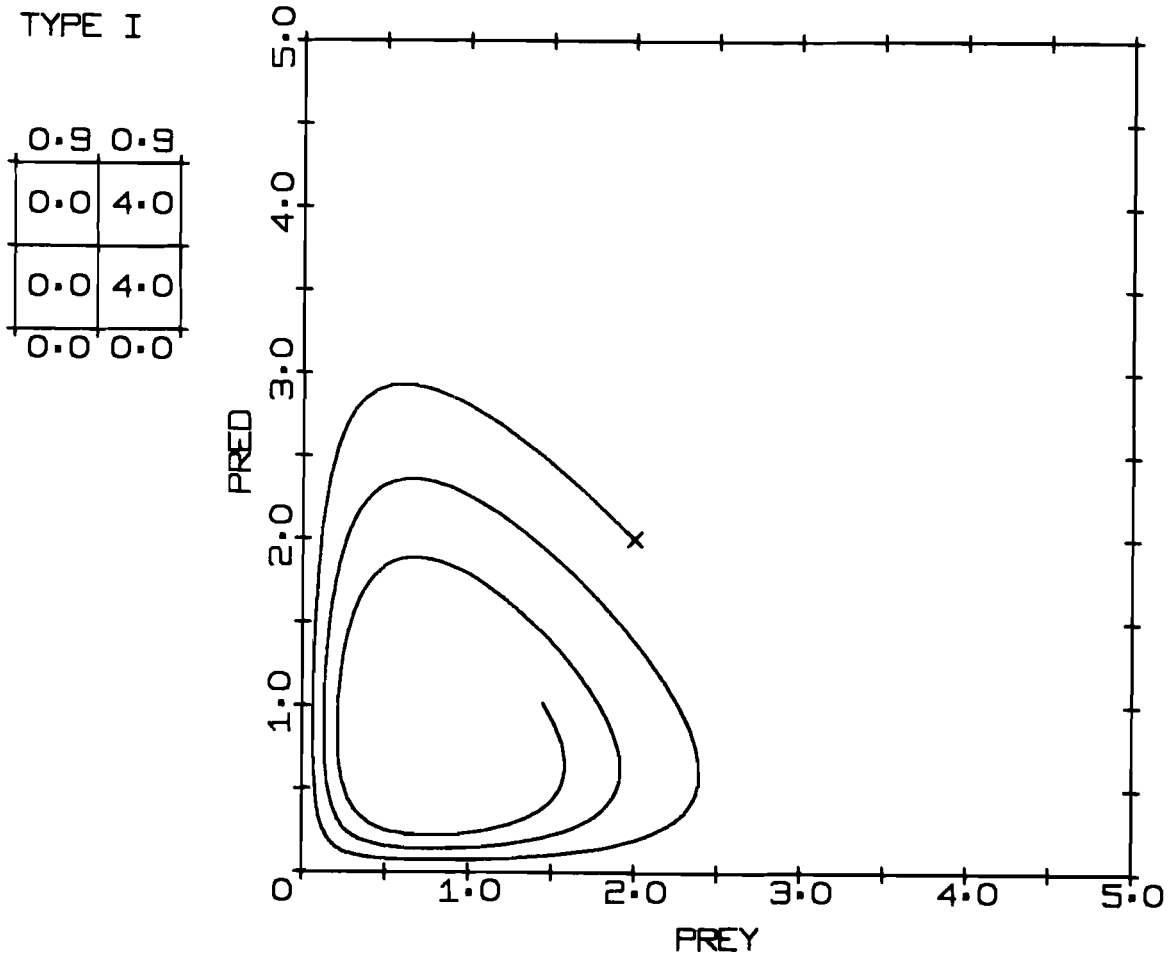


Figure 5. Two examples where neutral stability is destroyed.

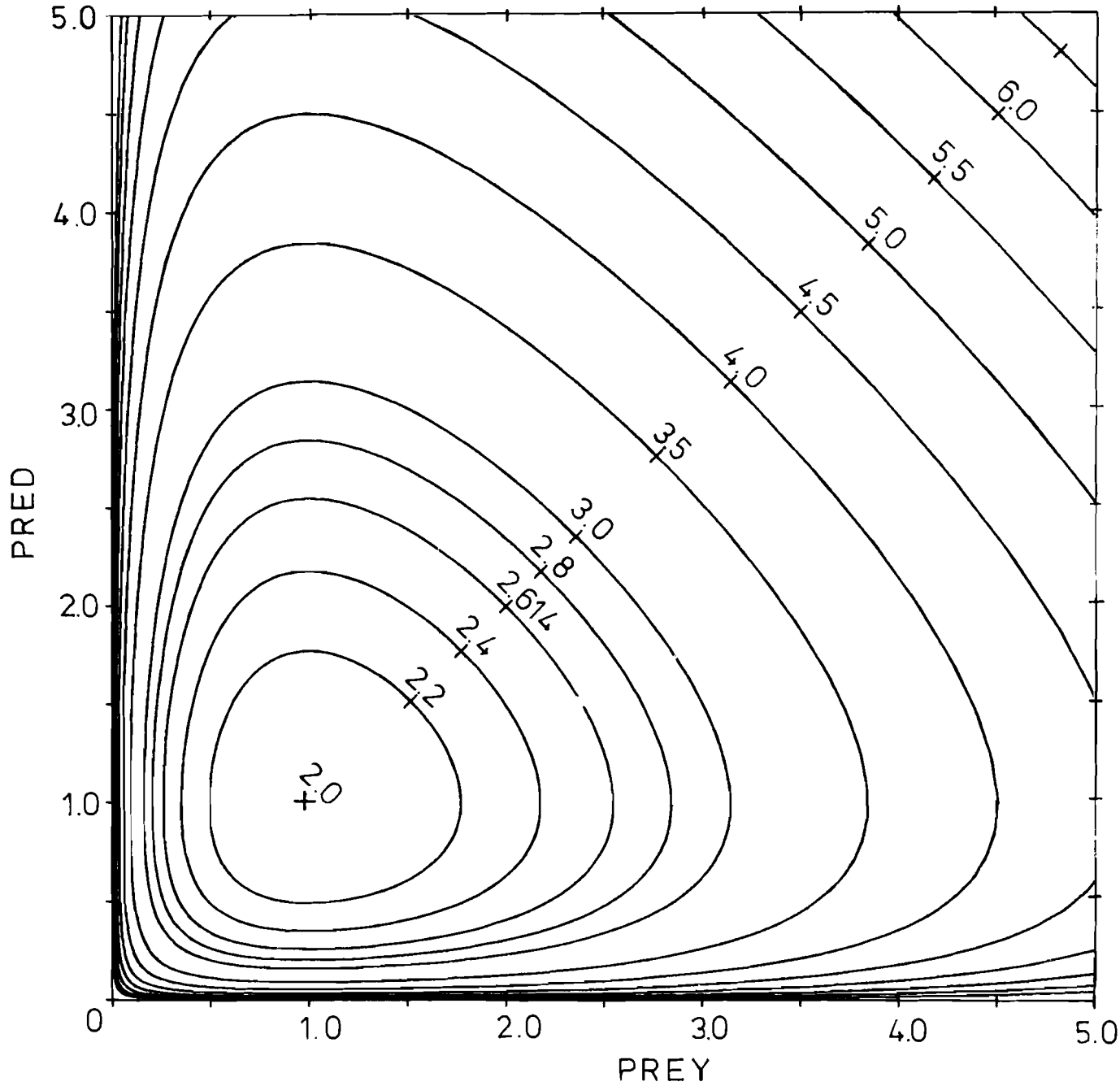
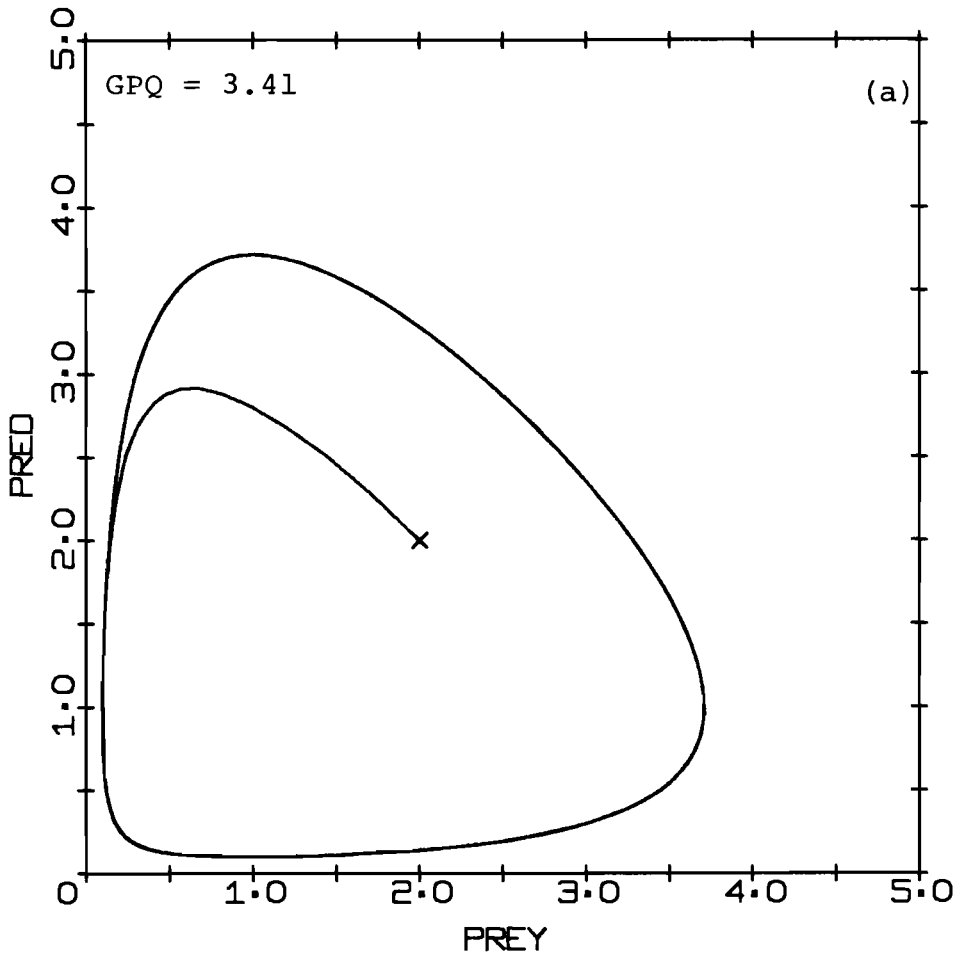


Figure 6. Contour levels for function GPQ.

TYPE I

0.9	0.9
0.0	4.0
0.0	4.0
0.1	0.1



TYPE III

0.1	0.1
0.0	4.0
0.0	4.0
0.9	0.9

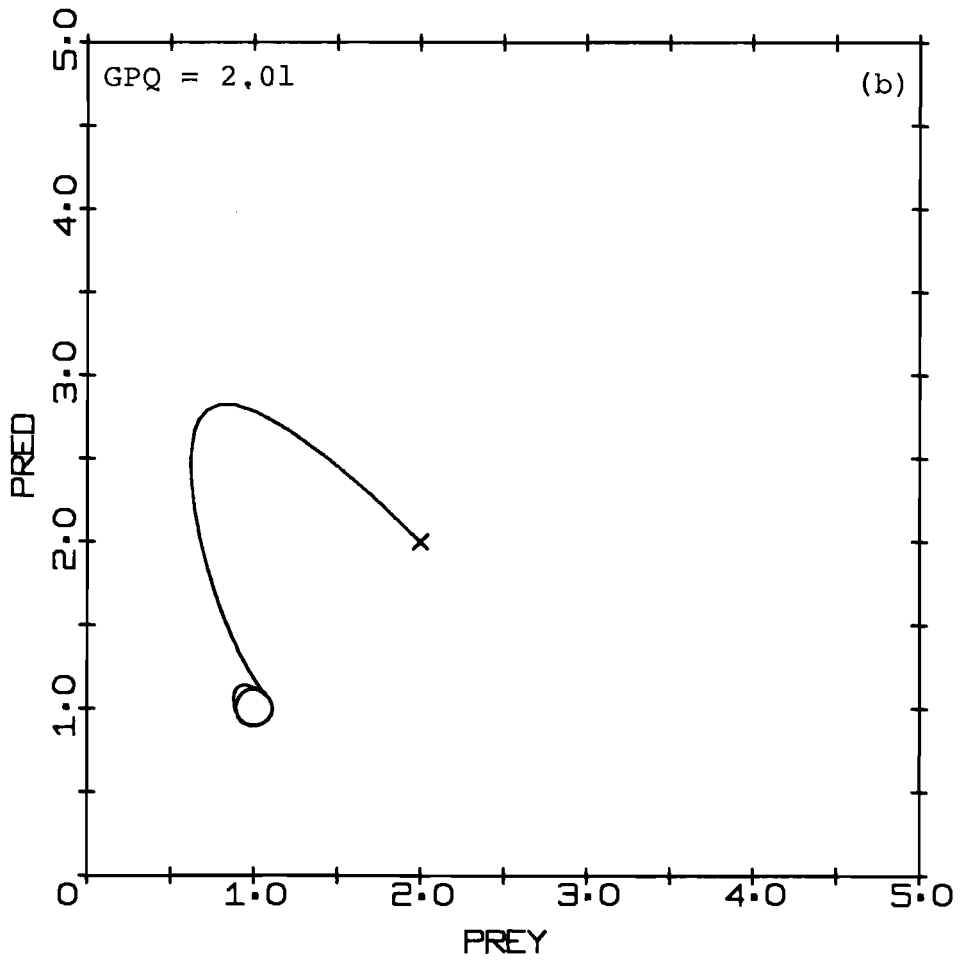
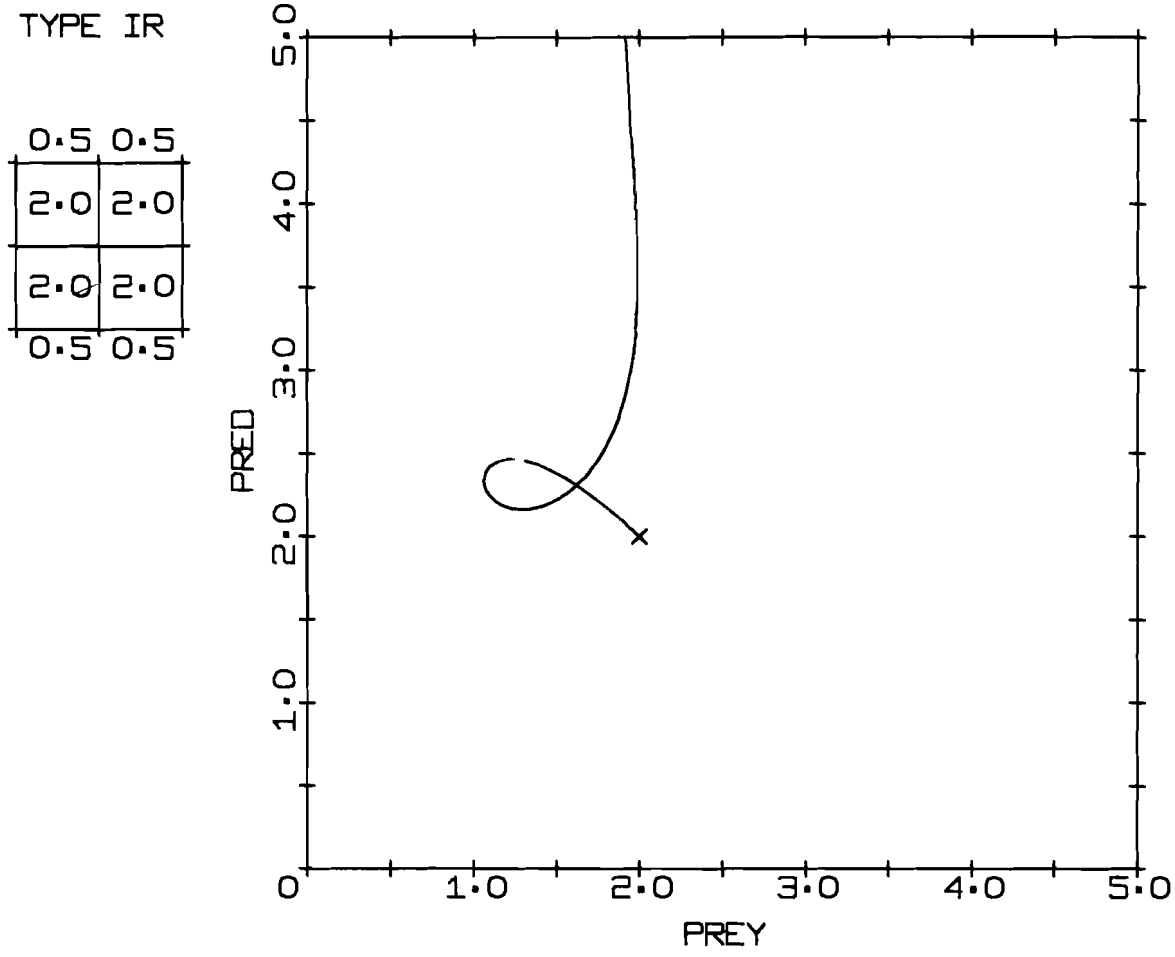


Figure 7. The two cases with the greatest dislocation of the final neutral orbit.



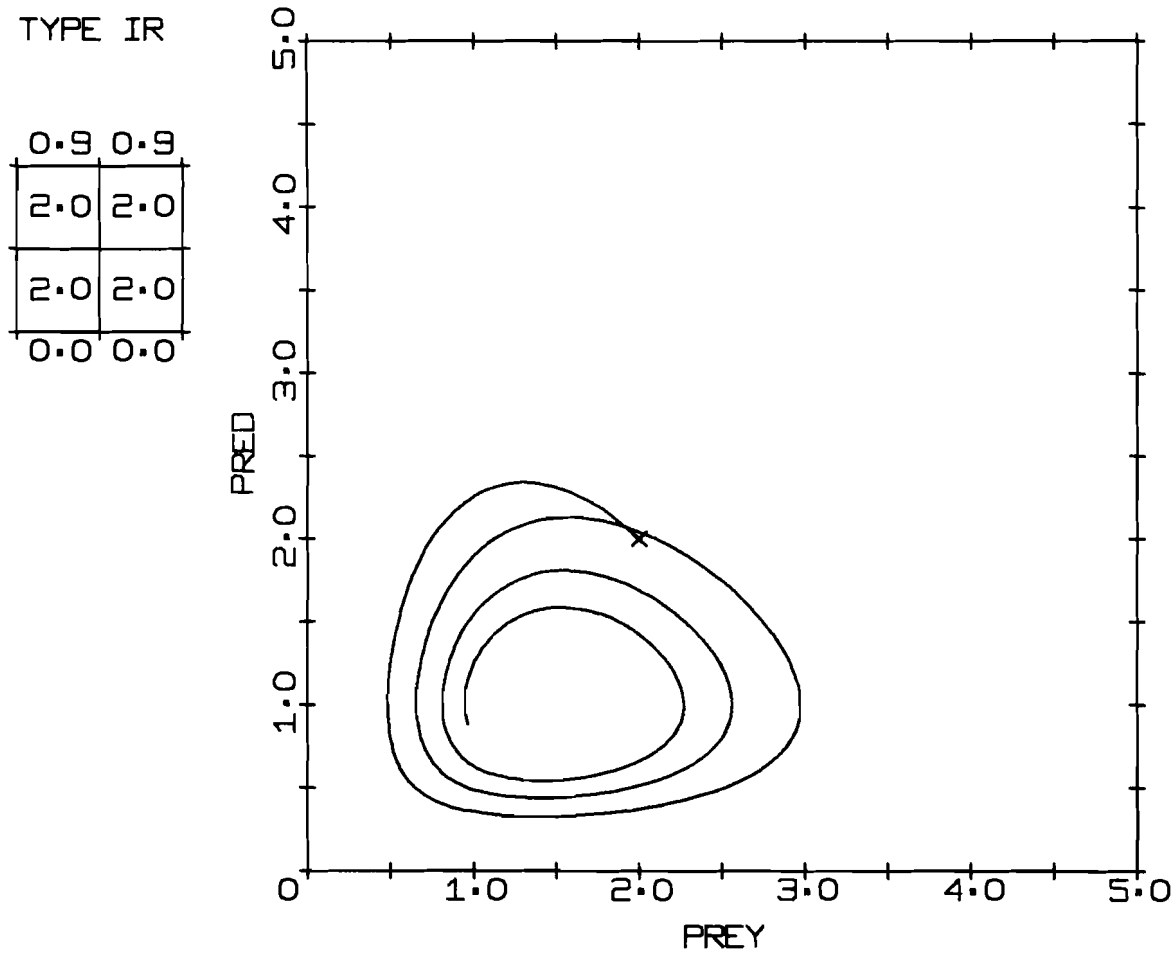


Figure 8. Some typical behavior for the system in the "refuge" configuration

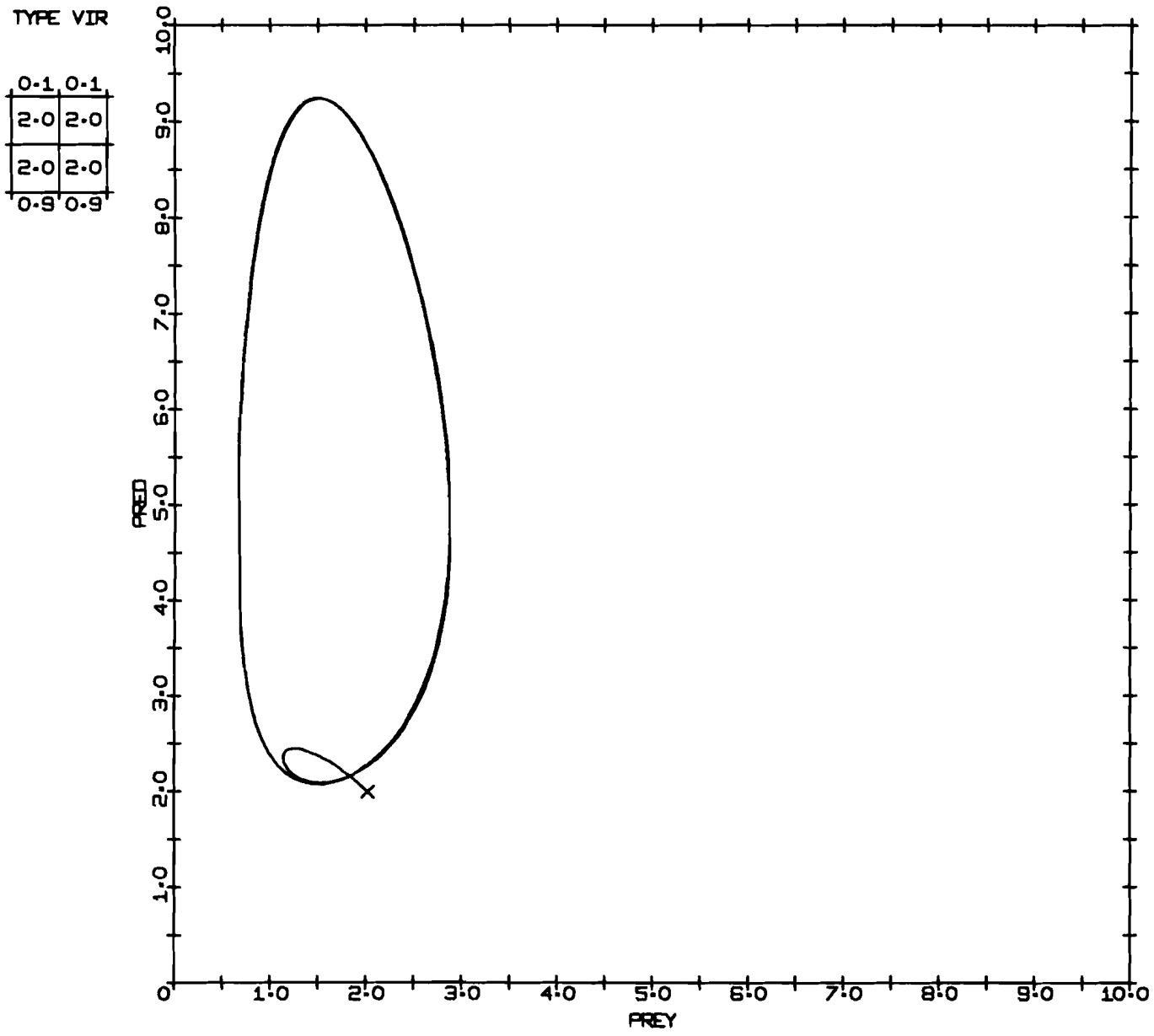
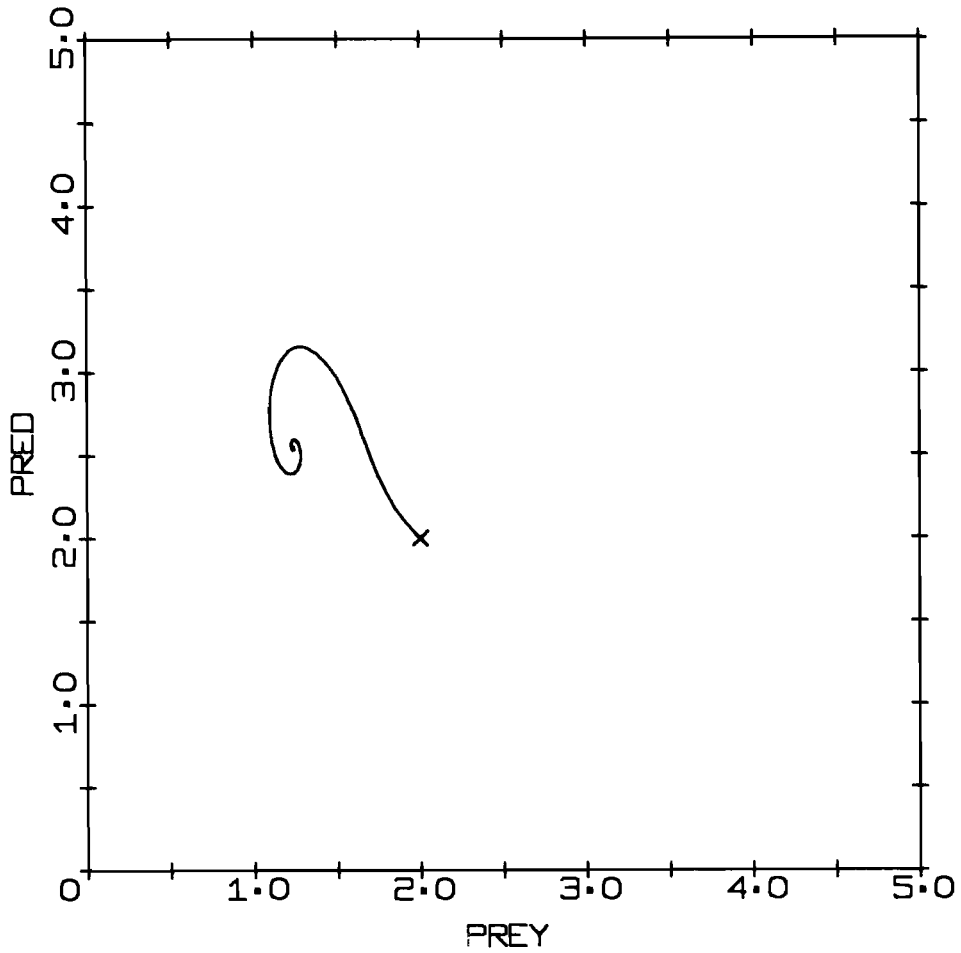


Figure 8. (continued)

TYPE VIIR

0·1	0·1
2·0	2·0
2·0	2·0
0·9	0·9



TYPE VS

0·1	0·1
2·0	2·0
2·0	2·0
0·9	0·9

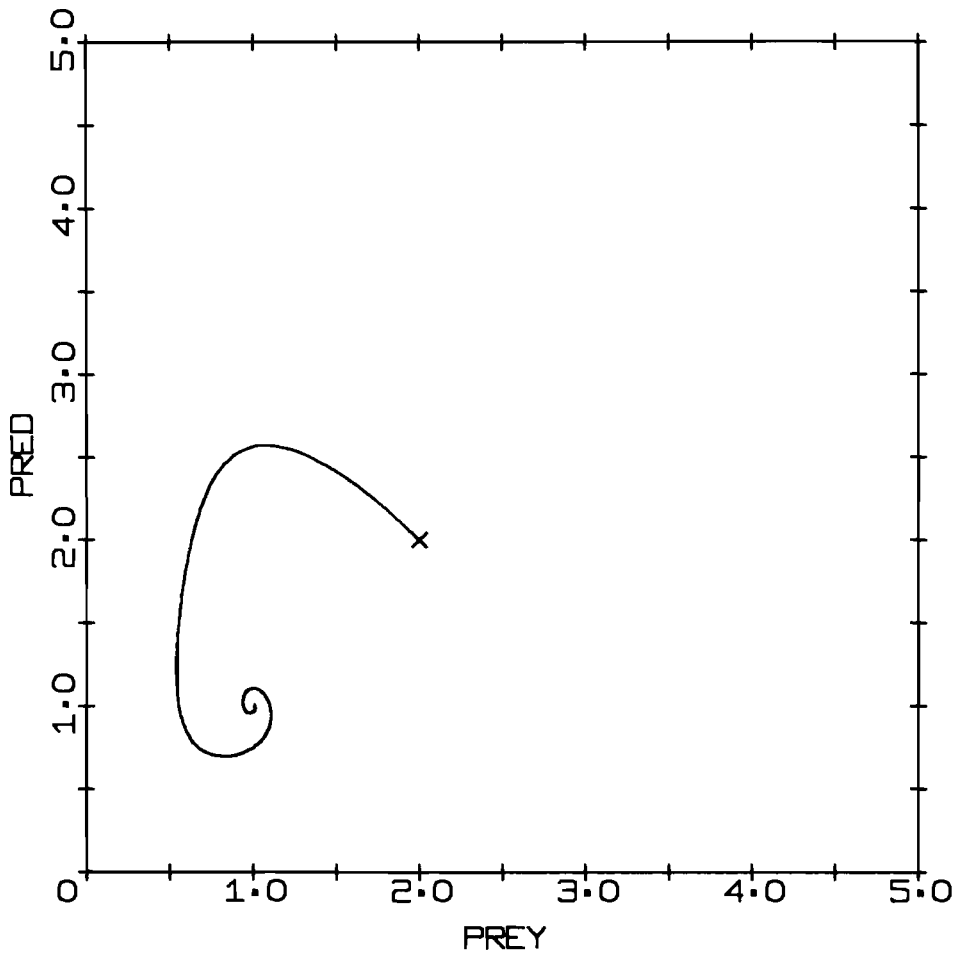


Figure 8. (continued)

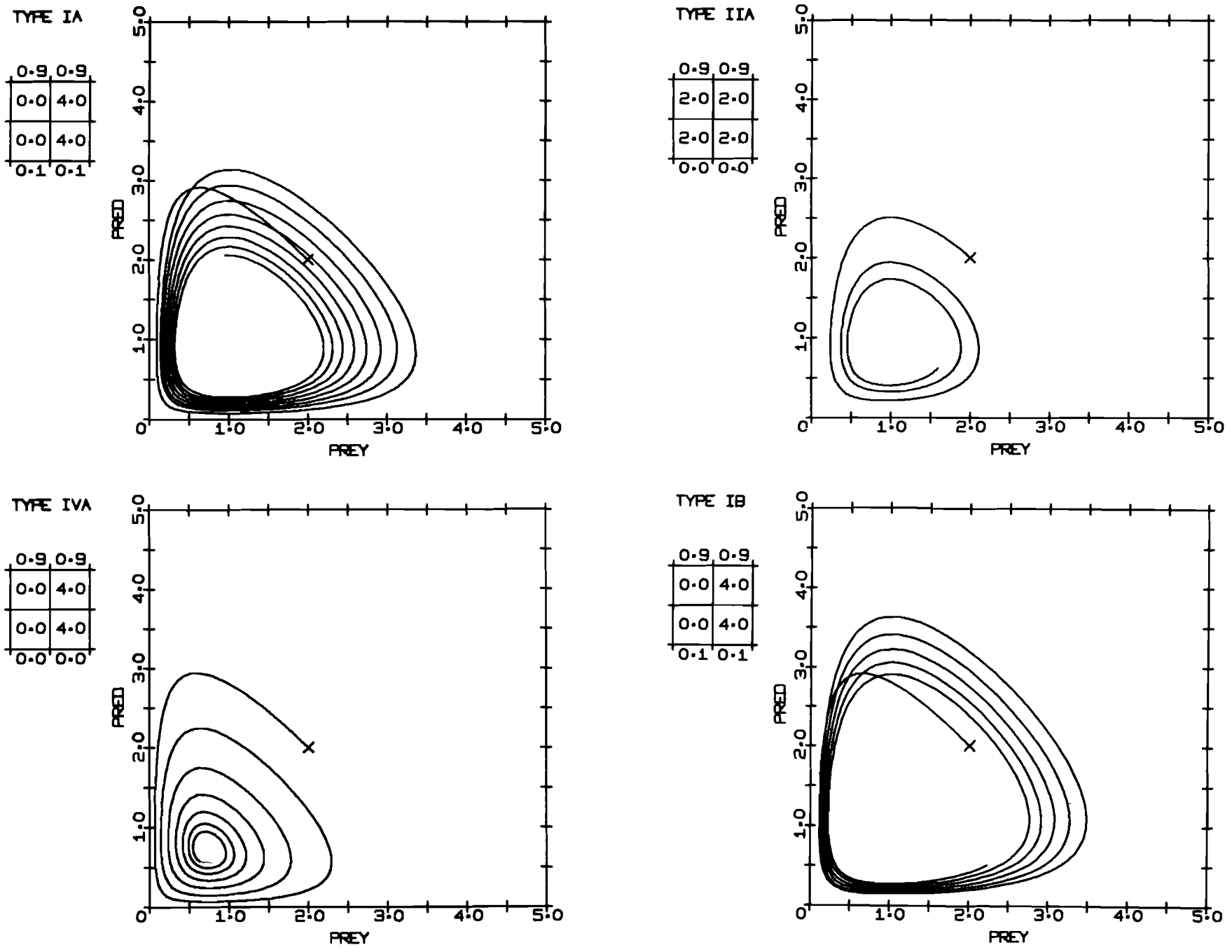
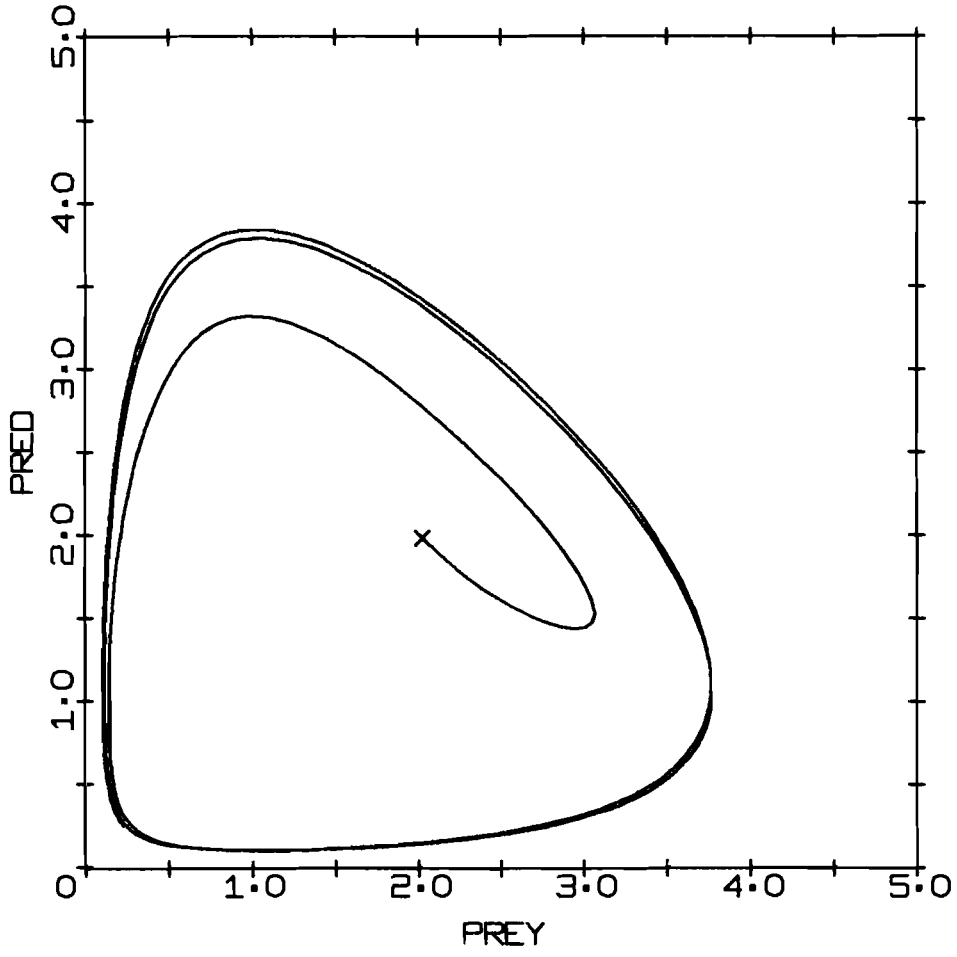


Figure 9. Four sample cases with the sites unequal. Stability is the rule.

TYPE IIIC

0·1	0·9
4·0	0·0
0·0	4·0
0·1	0·9



TYPE VID

0·1	0·1
0·0	4·0
0·0	4·0
0·9	0·9

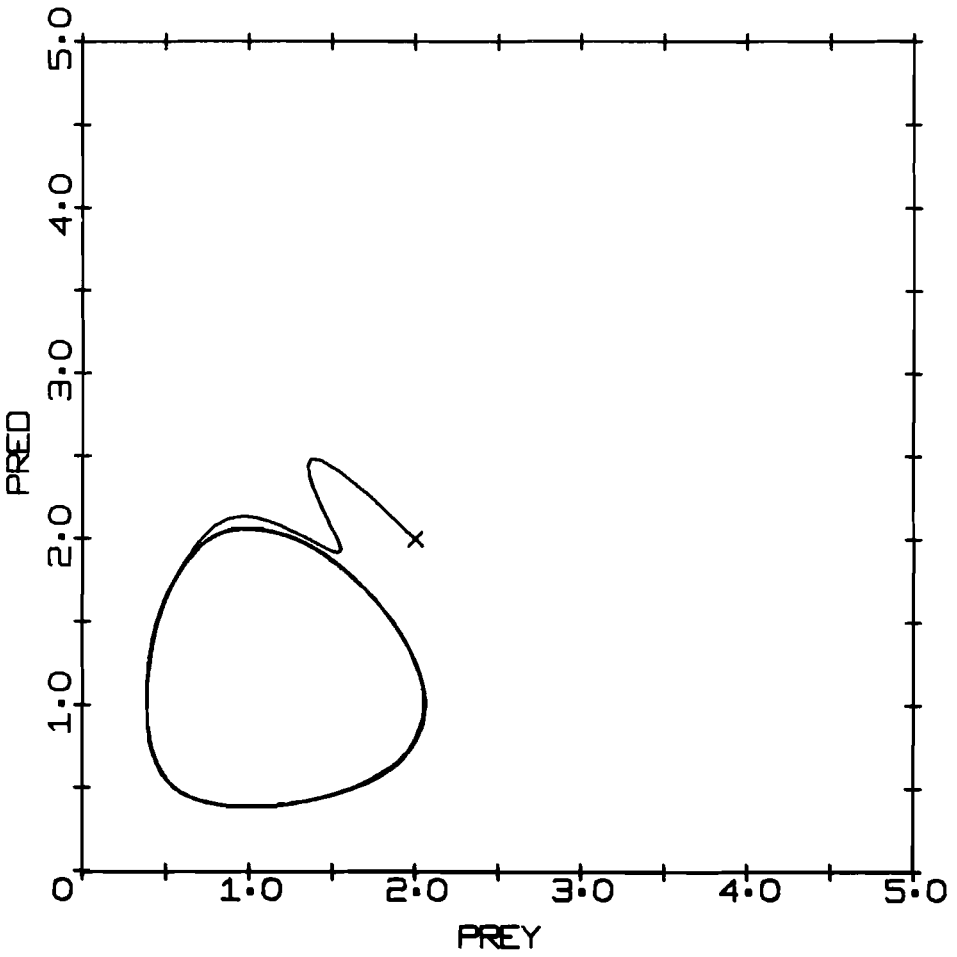
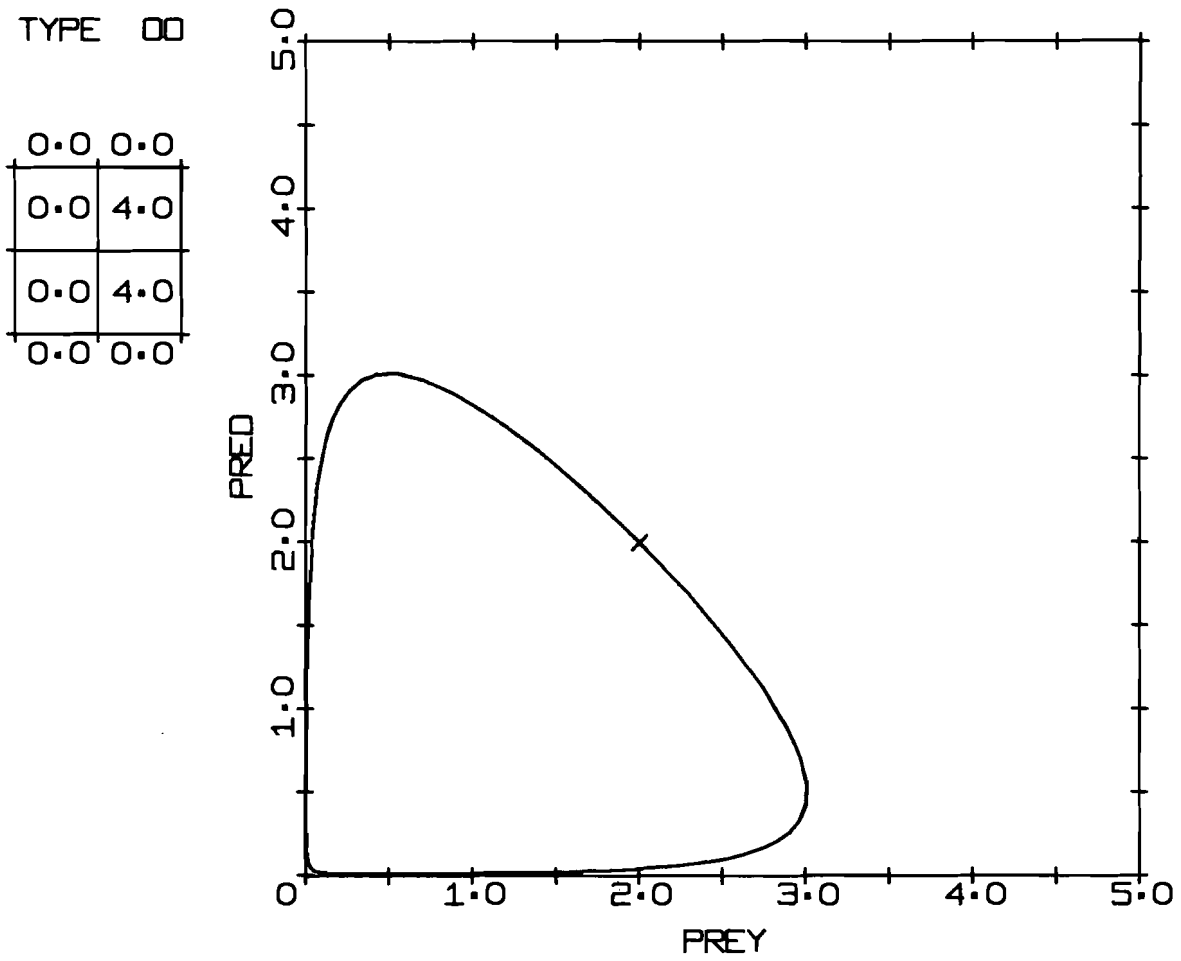


Figure 10. Typical behavior for Class C and D dispersal.



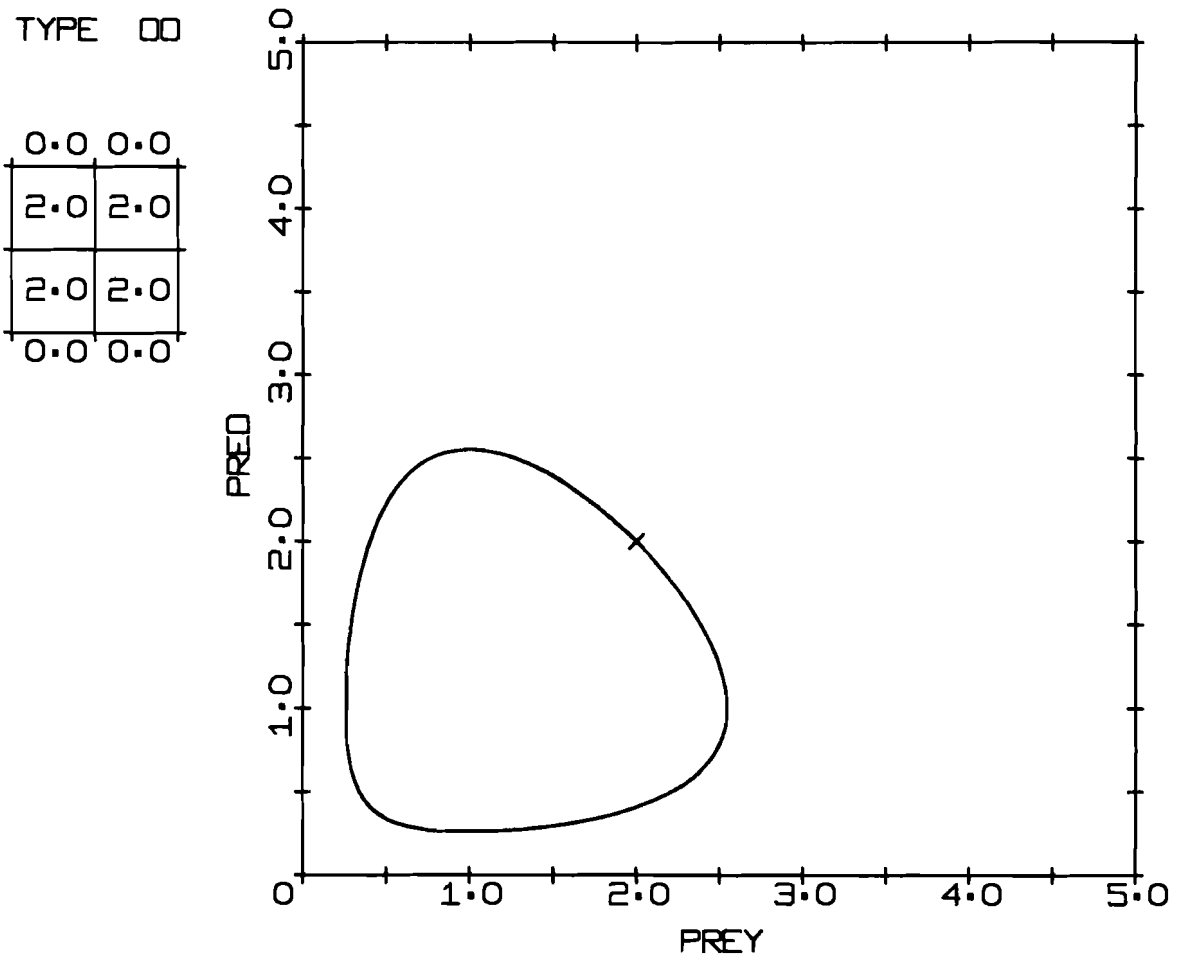


Figure 11. The effect of area on the L-V model. a) all animals are constrained to one site, but census is based on the entire area. b) animals equally distributed on both sites.

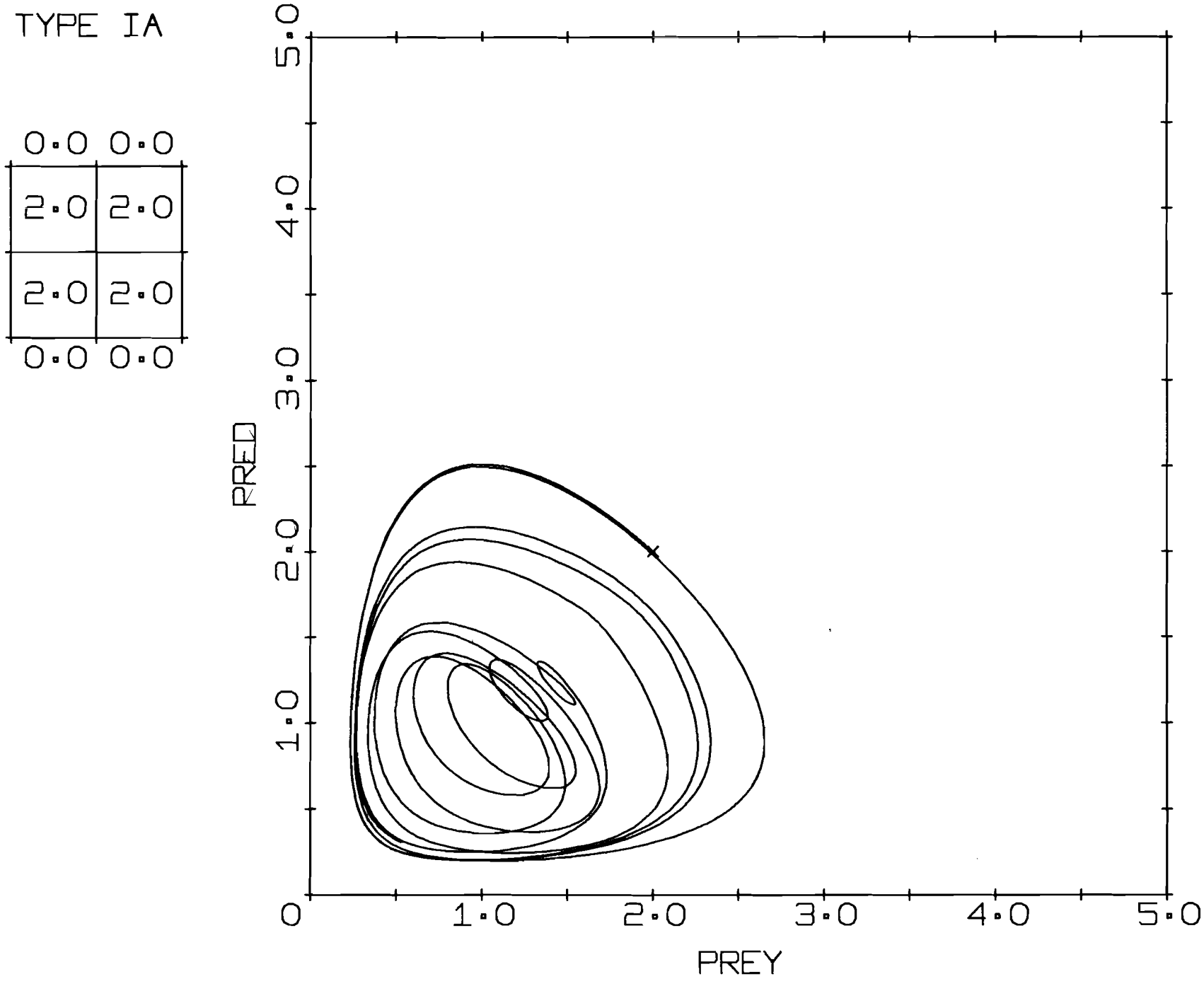


Figure 12. Phase trajectory of the population average for two slightly different and independent sites.

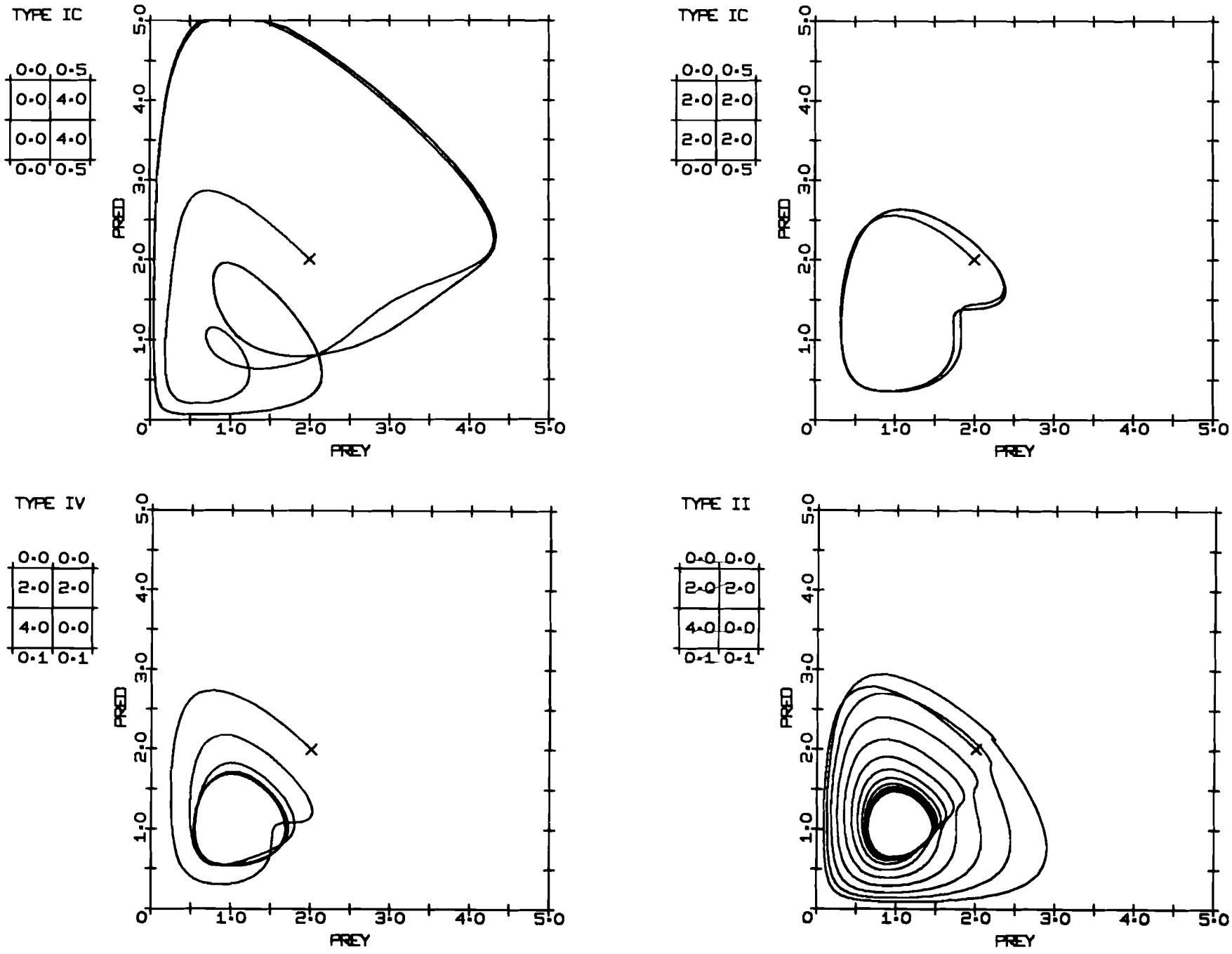
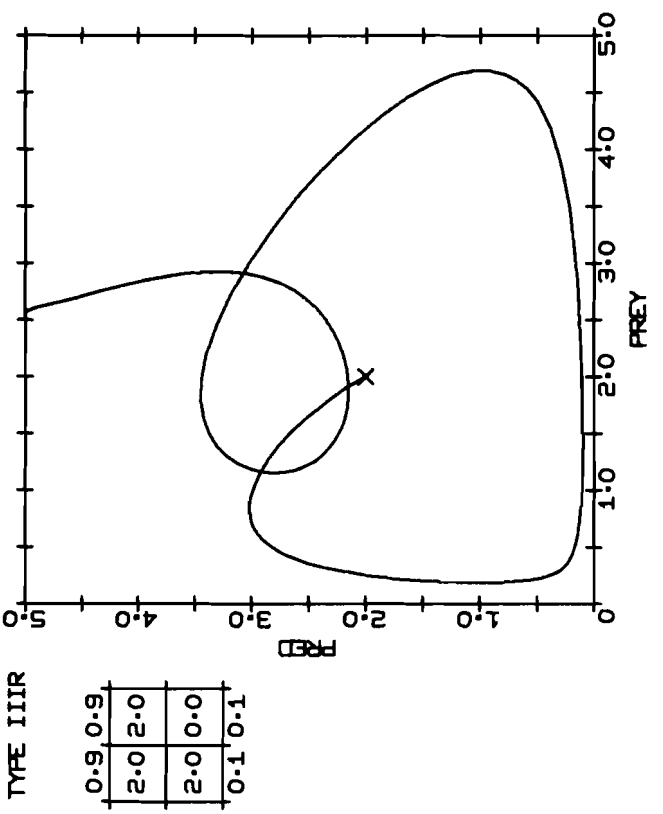
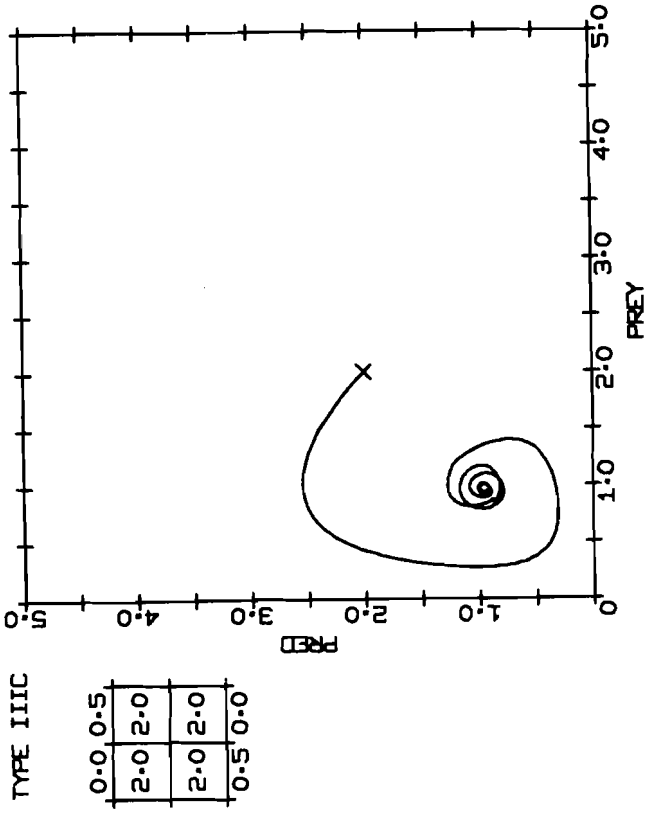
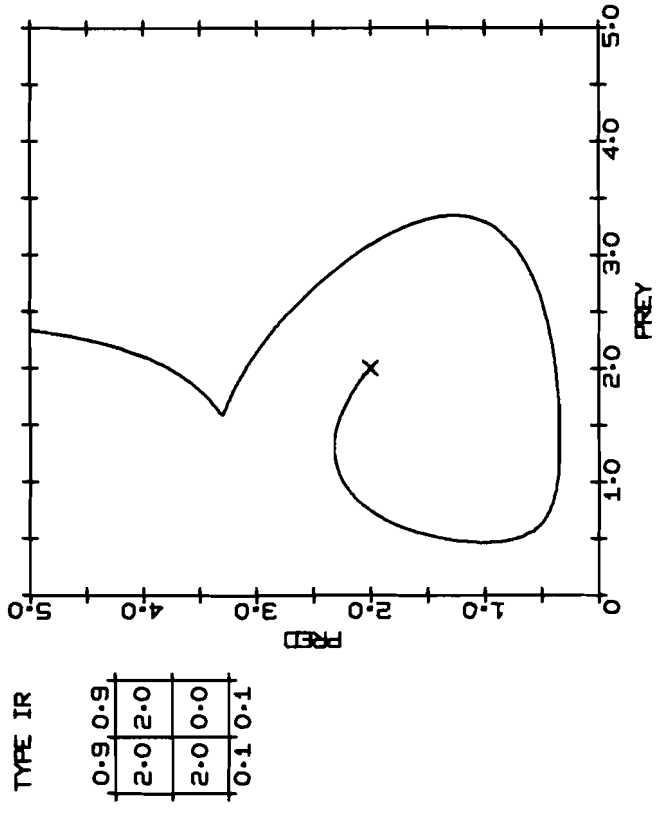
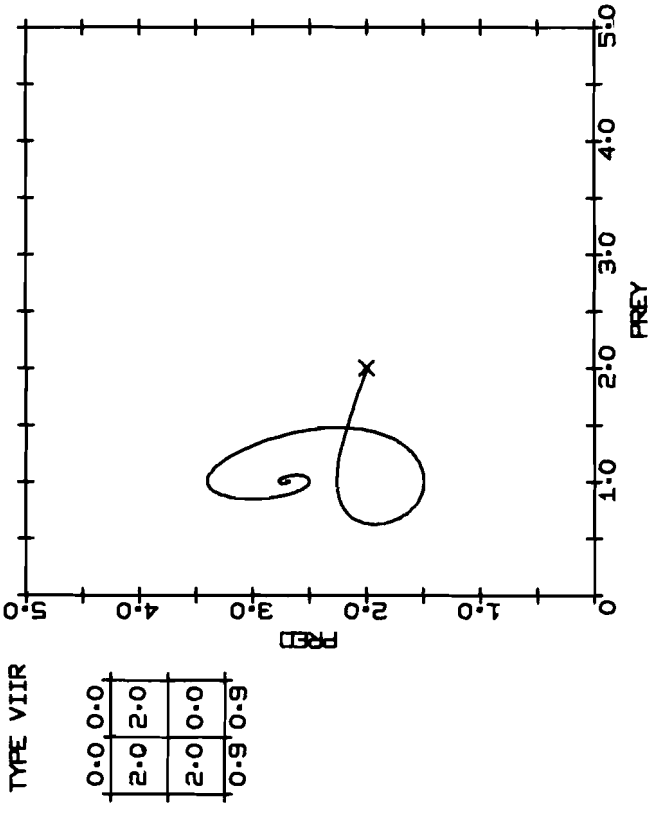


Figure 13. A collection of cases of pictorial interest.


TYPE IIIR
0.9 0.9
2.0 2.0
2.0 0.0
0.1 0.1
PREY
PRED
0
1.0
2.0
3.0
4.0
5.0


TYPE IIIC
0.0 0.5
2.0 2.0
2.0 2.0
0.5 0.0
PREY
PRED
0
1.0
2.0
3.0
4.0
5.0


TYPE IR
0.9 0.9
2.0 2.0
2.0 0.0
0.1 0.1
PREY
PRED
0
1.0
2.0
3.0
4.0
5.0


TYPE VIIR
0.0 0.0
2.0 2.0
2.0 0.0
0.9 0.9
PREY
PRED
0
1.0
2.0
3.0
4.0
5.0

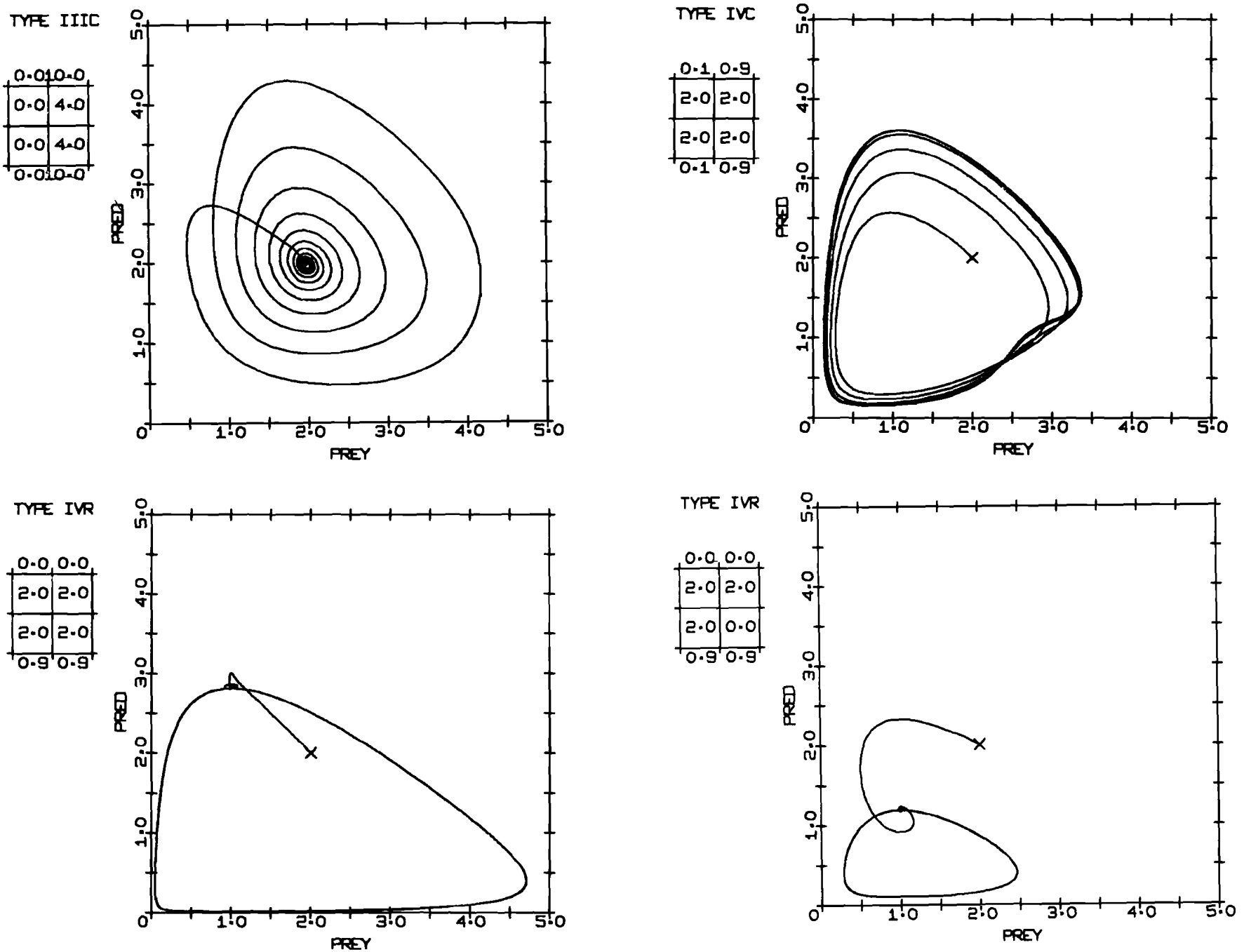


Figure 13. (continued)

References

1. Gause, G.F. (1934) The Struggle for Existence. Williams and Wilkins, Baltimore.

2. Granger, C.W.J. (1969) Spatial Data and Time Series Analysis. In S.J. Scott (ed) Studies in Regional Science. London.

3. Hirsch, M.W. and S. Smale. (1974) Differential Equations, Dynamical Systems and Linear Algebra. Academic Press, New York.

4. Huffaker, C.B. (1958) Experimental Studies on Predation: Dispersion Factors and Predator-Prey Oscillations. Hilgardia 27: 343-383

5. Jones, J.S. (1973) Ecological Genetics and Natural Selection in Molluscs. Science 182: 546-552.

6. Kerner, E.H. (1972) Gibbs Ensemble: Biological Ensemble. Gordon and Breach, New York.

7. Luckinbill, L.S. (1973) Coexistence in Laboratory Populations of Paramecium Aurelia and its Predator Didinium Nasutum. Ecology 54: 1320-1327.

8. Mac Arthur, R.H. and E.O. Wilson. (1967) The Theory of Island Biogeography. Princeton University Press, Princeton.

9. Mc Donald, J.F. and F.J. Ayala. (1974) Genetic Response to Environmental Heterogeneity. Nature 258: 572-574.

10. May, R.M. (1973) Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton.

11. Maynard Smith, J. (1974) Models in Ecology. Cambridge University Press, Cambridge.

12. Simberloff, D.S. and E.O. Wilson. (1970) Experimental Zoogeography of Islands: A Two-Year Record of Colonization. Ecology 51: 934-937.

13. Steele, J.H. (1974a) Spatial Heterogeneity and Population Stability. Nature 248: 83

14. Steele, J.H. (1974b) Stability of Plankton Ecosystems. In M.B. Usher and M.H. Williamson (eds) Ecological Stability. Chaoman and Hall, London.